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ON FOUR EIGHT-COMBED CHINESE BAT-FLEAS OF THE GENUS *ISCHNOPSYLLUS* IN THE COLLECTION OF THE BRITISH MUSEUM (NATURAL HISTORY)

BY KARL JORDAN

(With 18 Figures in the Text)

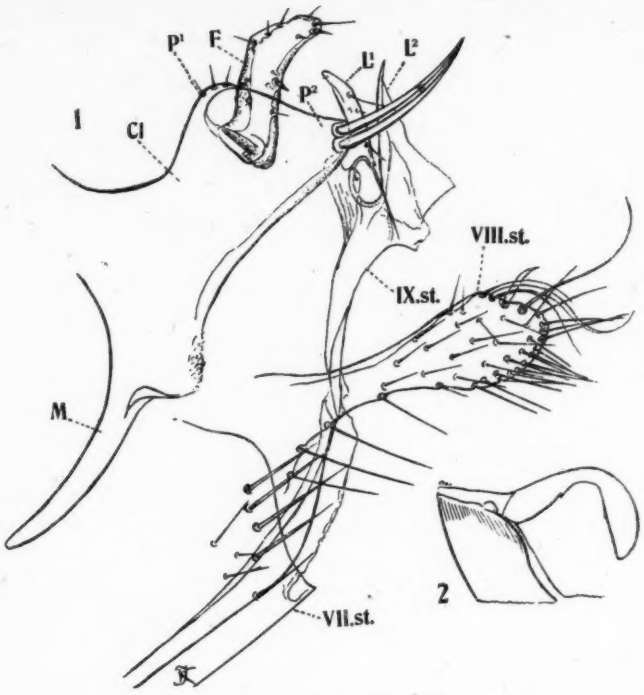
AN *Ischnopsyllus* Westw., 1833, lately sent by Miss Kuei-Chen Li, National Kweiyang Medical College, China, differs considerably from all the known *Ischnopsyllus* and suggests that the species are as numerous in China as in Europe. Inclusive of Miss Li's specimens four eight-combed species from China are represented in the British Museum, all that have so far been described from that country. We are much indebted to Miss Li for the new species and to Mr Yin-ch'i Hsü for paratypes of two bat-fleas described by him.

Up to the end of the last century (1898) the European eight-combed *Ischnopsyllus* were all considered by experts to belong to one species, the distinctions having escaped the various authors who had studied these fleas. Judging from the descriptions of Chinese bat-fleas published by Hsü and the specimens he kindly sent me, the same fate may be in store for the Chinese bat-fleas during the early period of research in systematics by Chinese students of the fauna of their country. A description of the new species and remarks on the distinctions of the three others may, therefore, be of some help to a beginner in entomology who does not yet know the details of structure which differentiates one *Ischnopsyllus* from the other, the species being much alike in general appearance and therefore easily intermixed if insufficient attention is paid to detail. In some cases we cannot even now distinguish with certainty the females of species in which the males are clearly distinct.

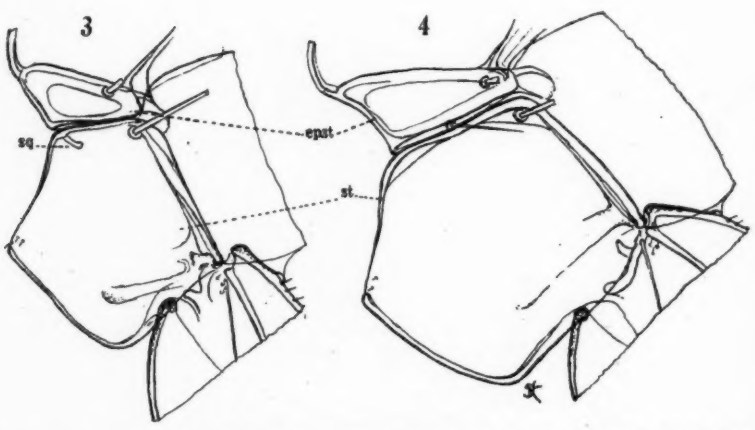
The four Chinese species before me fall into two groups:

I. Preoral tuber long and narrow, more or less as in *I. hexactenus* Kolen., 1856 (Fig. 2). Metasternite with squamulum (*sq.*, Fig. 3) at or near upper anterior corner. ♂ genitalia (Figs. 1, 5) of the *hexactenus* type: digitoid (*F*) narrow, elbowed dorsally, apical portion directed distad; apex of sternum IX divided into two lobes, anterior lobe pointed (L^1), ventrally with rounded sinus, at the distal side of which there is a short cone bearing a bristle; tendons of sternum IX and phallosome (*Pen*) long, making at least two convolutions; mantle (*Mt*) of phallosome narrow, concave dorsally for the greater part, apex turned up. *I. comans* Jord. & Roths., 1921, and *I. indicus* Jord., 1931.

II. Preoral tuber (Figs. 7, 11–13) broader, shorter, especially in ♀♀. Metasternite without squamulum (Figs. 4, 8). ♂ genitalia (Figs. 6, 17): digitoid narrow at base, much broader distally, in the Chinese species distal half elliptical; anterior apical lobe of sternum IX broadish, truncate; tendon of sternum IX making about half a convolution, those of the phallosome little



Figs. 1, 2. Fig. 1. *Ischnopsyllus indicus.* Male genitalia. Fig. 2. *I. indicus.* Preoral tuber.



Figs. 3, 4. Fig. 3. *Ischnopsyllus indicus.* Sternum and episternum of metathorax of female. Fig. 4. *I. liae* sp.nov. Sternum and episternum of metathorax.

more than one convolution; mantle (*Mt*) of phallosome with the dorsal margin for the greater part straight, posteriorly convex, apex not turned up. *I. needhamia* Hsü, 1935, and a new species. To this group belong all the European eight-combed *Ischnopsyllus*.

The preoral tuber is not quite constant in shape and sometimes slenderer in ♂ than in ♀ (Figs. 11–13). The presence of the metasternal squamulum in some bat-fleas and absence in others is of interest. This small sclerite, which lies in the membrane closing the metasternite in front and connecting it with the mesosternite, is missing in the European eight-combed *Ischnopsyllus* as a rule; but as I have found it in a few of our specimens of *I. octactenus* Kolen., 1856 and *I. dolosus* Dampf, 1912, we may expect it to occur very occasionally in all eight-combed *Ischnopsyllus*. It is absent from the few specimens we have of *I. emminus* Jord. & Roths., 1921, from South Africa, and present in all the six-combed *Ischnopsyllus*. It is absent from the Australian species described as *Ischnopsyllus*. The squamulum is evidently a functionless remnant and on the verge of extinction in eight-combed *Ischnopsyllus*. It would be interesting to find a specimen of a six-combed *Ischnopsyllus* devoid of the squamulum. Though the sclerite is not quite reliable for diagnostic purposes, it is nevertheless of some use in the determination of species.

(1) **Ischnopsyllus comans** Jord. & Roths., 1921

♂. On mesonotum eight dorsal subapical bristles much prolonged (not six as stated in the original description). Ventral arm of sternum VIII nearly as in *I. hexactenus*, about six times as long as its middle portion is broad, distally widened, apex curved upwards, ventrally obliquely rounded, the dorsal angle acute with the tip rounded off, apical and subapical bristles numerous, some of the apical ones very long. Digitoid three times as long as broad, apically much less extended backwards than in *I. hexactenus*.

♀. Stylet short, only twice as long as broad.

In the British Museum from: Pekin, on *Pipistrellus planeyi*, 1 ♂ (type), 1 ♀ (paratype) (M. Planey); Tsinan (Tsi-Nan-Fu), on *Leuconoë taiwanensis*, one pair, and on bat no. 95, 1 ♀, July 1926 (Dr E. Hindle).

(2) **Ischnopsyllus indicus** Jord., 1931 (Figs. 1–3, 5)

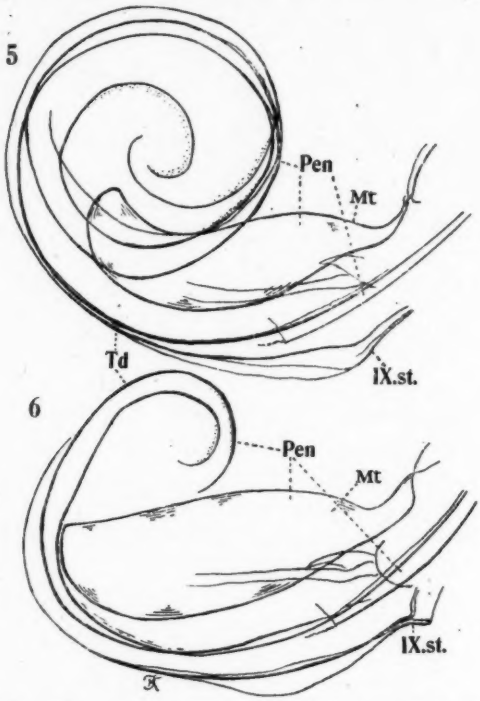
Ischnopsyllus needhamia Hsü, 1935, partim.

Described from two North Indian ♀♀. We have since received both sexes from Ceylon and China. Fig. 2 represents the preoral tuber.

♂. The genitalia (Fig. 1, taken from a Ceylonese specimen) differ from those of *I. comans* particularly in sterna VIII and IX and the digitoid: ventral arm of sternum VIII narrow proximally and widening distally, resembling a battledore, the elliptical distal area setiferous; uppermost apical bristle thin, below it on inner side a long broad pale one, followed by a short broad pale bristle, below which there is a long, more strongly sclerified non-broadened bristle;

from this point down more than a dozen shorter bristles. Digitoid (*F*) of clasper slenderer than in *I. comans*, the subbasal spiniform of posterior margin absent, the apex more produced. Manubrium (*M*) of clasper and the two apical lobes of sternum IX narrower. Tendons long (Fig. 5, taken from Soochow ♂).

♀. Stylet more than three times as long as broad. Fig. 3 represents the episternum and sternum of the metathorax of a ♀ from Nanking.



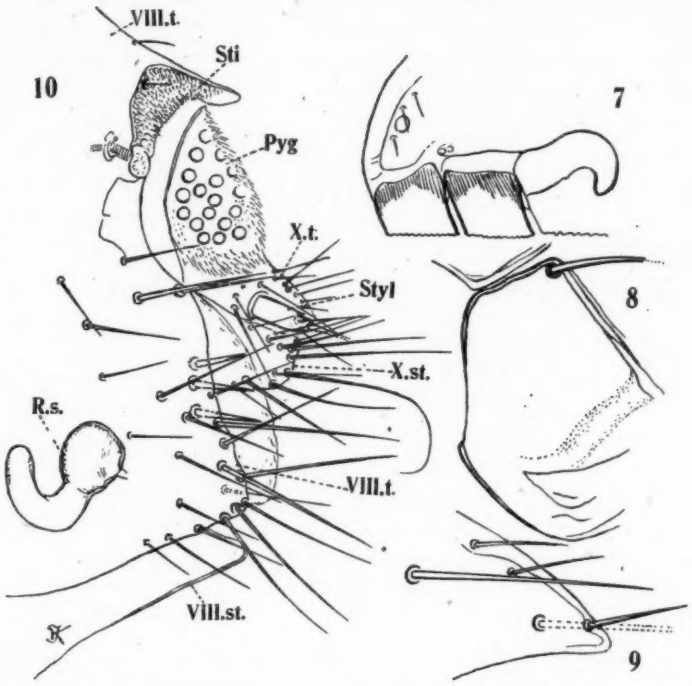
Figs. 5, 6. Fig. 5. *Ischnopsyllus indicus*. Portion of genitalia of male.
Fig. 6. *I. liae* sp.nov. Portion of genitalia of male.

In the British Museum from: North India, Dinga Gali, on *Barbastella darjeelingensis*, 1 ♀ (type); Ceylon, West Haputale, Ohiya, 6000 ft., February 1933, on *Pipistrellus* sp., 1 ♂, 3 ♀♀ (W. W. A. Phillips); China, Foochow, on *Rhinolophus*, April 1922, 1 ♀ (C. R. Kellogg); Nanking, on bat, 2 ♀♀ (Dr H. M. Jettmar); Soochow, 1 ♂ paratype of *I. needhamia*, on bat (Yin-ch'i Hsü); Guam, on *Pipistrellus abramus*, 1 ♀ (Allan Owston).

(3) **Ischnopsyllus needhamia** Hsü, 1935 (Figs. 7–10)

The species was based on 7 ♂♂ and 9 ♀♀ found on bats 'collected from cracks and crevices in the local pagodas and temples' at Soochow. The bats were *Pipistrellus abramus*, *Nyctalus aviator* and *Rhinolophus ferrum-equinum*

nipponensis. The fleas were evidently not kept separate as to the species of bat on which they were found. On my suggestion of an exchange of specimens of the bat-fleas described by him against some Chinese fleas from the N. C. Rothschild collection, Mr Yin-ch'i Hsü very kindly sent me a pair of *I. needhamia*, and a ♂ of his *Ischnopsyllus wui*, 1936, which latter is *Nycteridopsylla galba* Dampf, 1910 (of which the type and a paratype are in the N. C. Rothschild collection). I am very grateful to Mr Hsü for thus assisting me. The pair sent as *needhamia* represents two species: the ♂ is *I. indicus*

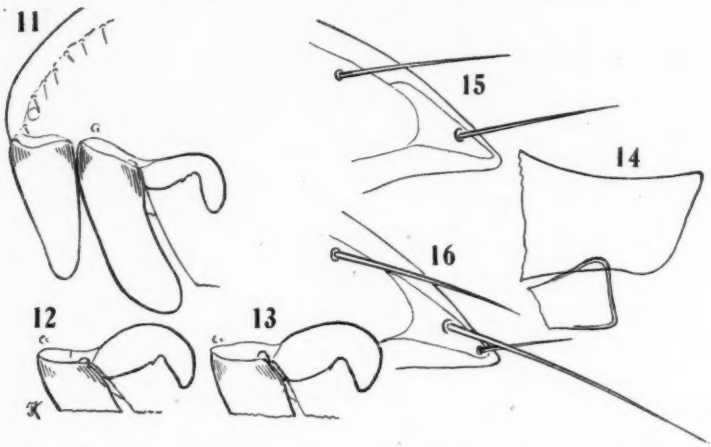


Figs. 7–10. Fig. 7. *Ischnopsyllus needhamia*. Preoral tuber of female. Fig. 8. *I. needhamia*. Metasternum of female. Fig. 9. *I. needhamia*. Tip of mesopleurite of female. Fig. 10. *I. needhamia*. Genitalia of female.

(see above), but the ♀ is evidently *needhamia*. Though Hsü's figures fall short of the standard introduced and improved since Julius Wagner took up the systematics of fleas about 50 years ago, they are certainly not valueless for the specialist, and the neatness of execution gives promise for the future. Hsü's Figs. 8 and 10 of the ♂ prove that the ♂ sent to me is not *I. needhamia* and that Hsü's species belongs to group II as characterized above, the mantle of the phallosome being broad, the tendons short, and the digitoid broad in distal half and narrow at base. Hsü's Fig. 8 further shows that the ♂ drawn (type

of *needhamia*) is different from the new species hereafter described: the narrower digitoid and the ventral bundle of long bristles (probably on sternum VIII) readily distinguish *I. needhamia* ♂. However, it is very desirable that the ♂-genitalia be redrawn on a larger scale, especially the digitoid and sternum VIII.

♀. The specimen received from Mr Hsü is similar to *I. intermedius* Roths., 1906 (but the ♂-genitalia are quite different): apical portion of preoral tuber (Fig. 7) narrower and much shorter than the horizontal portion. Genal process less strongly convex ventrally in front of oblique apical margin than in *I. intermedius* and the new species. Spines in combs 31, 25, 19, 25, 21, 16, 13, 10, these numbers being within the range of variability of *I. intermedius*.



Figs. 11–16. Fig. 11. *Ischnopsyllus liae* sp.nov. Preoral tuber of male. Figs. 12, 13. *I. liae*. Preoral tubers of two females. Fig. 14. *I. liae*. Genal process. Fig. 15. *I. liae*. Mesopleurite of male. Fig. 16. *I. liae*. Mesopleurite of female.

Mesonotum with more than 20 (I count 22) small bristles between the basal bristles and the posterior row; on each side five slender spines on inner surface. Above tip of mesopleurum (Fig. 9) near dorsal margin a shortish but rather stout bristle, in front of which there is a large bristle midway between dorsal and ventral margins (this large bristle broken on both sides of body), and further forward two shortish and rather thin subdorsal ones; in these bristles *I. needhamia* differs from the new species and resembles *I. intermedius*, in which the bristles of this sclerite are variable in size and number, but less variable in position. Metasternum (Fig. 8) shorter (in the horizontal sense) than in *I. intermedius* and sp.nov., its proportions practically the same as in *I. octactenus* Kolen., 1856 and *I. simplex* Roths., 1906, its dorsal margin being only a little longer than half the upper portion of the anterior margin. Metepisternum with one bristle, which is subapical.

Abdominal sternum VII with 10 bristles on one side and 13 on the other; its apical margin dorsally strongly rounded and subventrally slightly convex (the outline is somewhat distorted and therefore not drawn here). Cavity of stigma of segment VIII larger than in any of the allied species, reaching the dorsal margin of the segment (Fig. 10, *Sti*). From this stigma downwards on outer surface there are 22 bristles on each side inclusive of apical ones; on inner side three rather stout bristles and near ventral angle a long thin one. Stylet (*Styl*) with nearly parallel sides from base to small subapical bristle, broader than in *I. intermedius*, less than thrice as long as broad. Spermatheca

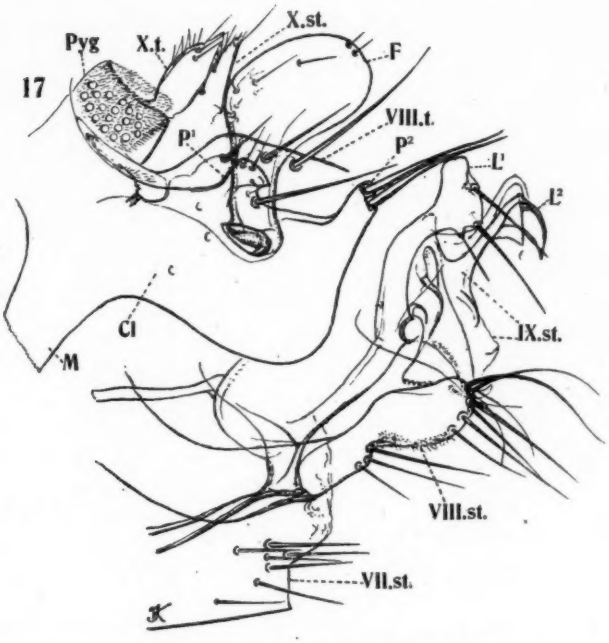


Fig. 17. *Ischnopsyllus liae*. Genitalia of male.

(*R.s.*) as in *I. intermedius*, its globular body smaller than in *I. octactenus*, *I. simplex* and sp.nov.; apex of its tail evenly rounded.

In a series of specimens all these details will be found variable to some extent as in other species of the genus.

Length: ♀ 3·0 mm., hind femur 0·5 mm. (Hsü gives as length of ♂ 2·3, ♀ 2·0 mm., which can hardly be correct; but the length of the flea depends much on the degree of contraction.)

China: Soochow; type and paratypes in collection Hsü, paratypes in collection Wu and one ♀ paratype in British Museum. Some of these paratypes are possibly *I. indicus* or even the new species. There are a few obvious slips

of observation in Hsü's description which it is hardly necessary for me to correct.

(4) **Ischnopsyllus liae** sp.nov. (Figs. 4, 6, 11–18)

Spines of combs more numerous than in the three Chinese species here dealt with: in ♂ 31, 25, 27, 29, 26, 23, 20, 17; in ♀♀ 32–33, 27–28, 25–29, 27–29, 25–24, 20–21, 20–17, 15–15 (all anterior figures belong to one specimen and the posterior ones to the other). Frons visibly more rounded above the spines than in the other species from China. Preoral tuber narrower in ♂ (Fig. 11) than in the two ♀♀ (Figs. 12, 13). Genal process (Fig. 14) more strongly rounded-dilated ventrally before oblique apical margin. Upper angle of maxilla less produced upwards than in *I. needhamia*. Mesopleurite of ♂

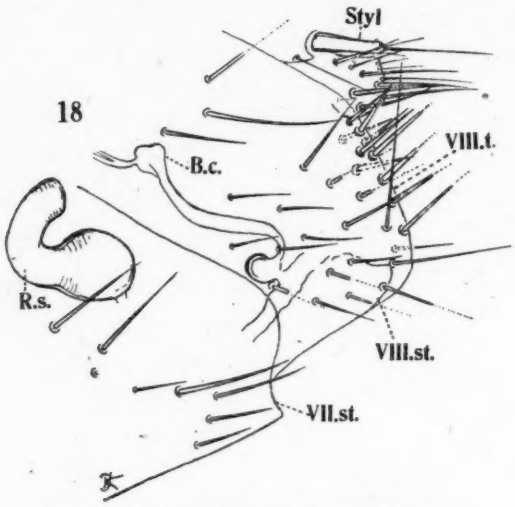


Fig. 18. *Ischnopsyllus liae*. Genitalia of female.

(Fig. 15) with a moderately long bristle at some distance from apical angle nearer dorsal than ventral margin, in the two ♀♀ (Fig. 16) a short bristle at apex with a very long one in front of it, this sex agreeing in these bristles with *I. indicus*, *I. comans* and *I. hexactenus* (in *I. octactenus* and close allies the small bristle is placed immediately above the long one). Sternum and episternum of metathorax (Fig. 4) longer than in *I. needhamia* and most other species of *Ischnopsyllus*, the upper margin of the sternum being about as long as the upper portion of the anterior margin; the same, somewhat variable, proportions obtain in *I. intermedius*; on episternum the usual long bristle near apex and an additional smaller one ventrally in or near middle as in *I. elongatus*, *I. intermedius* and *I. obscurus*. The range of individual variability of the bristles of the mesopleurite and metepisternum in *Ischnopsyllus* as regards number, position and size requires still to be ascertained.

Modified segments. ♂. Each side of sternum VII and tergum VIII with seven bristles. Sternum VIII very distinctive (VIII, *st.*, Fig. 17), its ventral margin abruptly incurved in middle and bearing in front of the sinus three bristles, beyond the sinus the margin rounded to dorsal apical angle, which itself is rounded off, apically and subapically four long marginal bristles on outside and two on inner, between the two sets of bristles numerous very small hairs at the ventral margin, dorsal margin convex a little beyond middle and on frontal and distal sides of this convexity shallowly incurved. Apical margin of clasper (*Cl*) with two processes, the upper one (P^1) short and rounded, with a sharp ventral nose, below which there is a round sinus, from this sinus to the lower process (P^2) the margin straight, oblique; P^2 a little longer than broad, with nearly parallel sides and obliquely truncate apex bearing the usual two stout bristles. Digitoid (*F*) narrow at base, apical half broad, elliptical and directed backwards, its bristles small, none spiniform. Manubrium (*M*) of clasper broad, gradually widening towards clasper. The two apical lobes of sternum IX also distinctive: upper lobe (L^1) first curved, with parallel sides, convex above, apical third directed upwards broadest ventrally, about thrice as long as apically broad, ventrally with a thin bristle on a cone, at ventral distal angle a larger bristle and a similar one on posterior margin above middle; lower lobe L^2 arising from a broad base, narrow, distally strongly widened and split into an outer and an inner flap (on both sides of body), both flaps curved down, ventral angle of each sharp, inner flap the longer and more sharply pointed one. Frontal two-thirds of mantle (*Mt*) of phallosome (*Pen*) (Fig. 6) dorsally almost straight, its anterior angle not curved up. Tendon of sternum IX making half a convolution, tendons of phallosome a little over one convolution. Sensilium (*Pyg*) of tergum IX almost a parallelogram in lateral aspect, its posterior margin probably divided by a sinus in centre between the backwards projections on right and left sides of body.

♀. Apical margin of sternum VII (Fig. 18) incurved subventrally, evenly rounded above this shallow sinus, with 14 bristles in one specimen and 18 in the other on the two sides together. On outer surface of tergum VIII from the stigma to ventral and apical margins in one specimen (off bat 359·1) 19 bristles on one side and 21 on the other, three of the apical ones being stout and rather short for their thickness, on inner side three short stout bristles; in second example (off bat 374·1) 25 on one side, 27 on the other, five apical ones stout, on inner side four stout bristles; in both specimens the inner bristles shorter and thinner than the stout outer ones. Stylet thrice as long as broad (bat 359·1) or four times (bat 374·1). Spermatheca as in *I. indicus*, apex of tail truncate-rotundate (duct destroyed by maceration in both specimens).

Length: ♂ 2·2 mm., ♀ 2·7–3·0 mm.; hind femur: ♂ 0·39 mm., ♀ 0·46–0·47 mm.

China, Kweiyang, on bat 359·1 one pair, on bat 374·1 one ♀, received from Miss Kuei-Chen Li, in whose honour the species is named.

The references to the literature concerning different species of *Ischnopsyllus* and *Nycteridopsylla* are as follows:

Ischnopsyllus Westw., 1833, *Ent. Mag.* **1**, 362.
I. comans Jord. & Roths., 1921, *Ectoparas.* **1**, 143, Text-figs. 118–121.
I. dolosus Dampf, 1912, *Rev. Russe Ent.* **12**, 43, Text-fig. 1.
I. emminus Jord. & Roths., 1921, *Ectoparas.* **1**, 142, Text-figs. 116, 117.
I. elongatus Curtis, 1832, *Brit. Ent.* p. 417, Pl. (as *Ceratopsyllus*).
I. hexactenus Kolen., 1856, *Paras. Chiopt.* p. 31 (as *Ceratopsyllus*).
I. intermedius Roths., 1898, *Nov. Zool.* **5**, 543, Pl. 17, Fig. 15 (as *Ceratopsylla*).
I. needhamia Hsü, 1935, *Peking N.H. Soc. Bull.* **9**, 293, Figs. 7–11 on Pl.
I. obscura Wagner, *Hor. Soc. Ent. Ross.* **31**, 584, Pl. 9, fig. 21 (as *Ceratopsylla*).
I. octactenus Kolen., 1856, *Paras. Chiropt.* p. 31 (as *Ceratopsyllus*).
I. simplex Roths., 1906, *Nov. Zool.* **13**, 186.
Nycteridopsylla Oudem., 1906, *Tijdschr. Ent.* **49**, Verslag, p. 58.
N. galba Dampf, 1900, *Zool. Anz.* **36**, 11, text-figs. 1, 2.
N. wui Hsü, 1936, *Peking N.H. Soc. Bull.* **10**, 137, Fig. (as *Ischnopsyllus*).

Lettering to figures

B.c. bursa copulatrix; *Cl*, clasper; *epist.* episternum; *F*, digitoid; L^1 and L^2, apical lobes of sternum IX; *M*, manubrium of clasper; *Mt*, mantle of lamina of phallosome; P^1 and P^2, dorsal and ventral apical angles of clasper; *Pen*, phallosome; *Pyg*, sensilium of tergum IX; *R.s.* spermatheca; *st*, sternum; *Sti*, stigma; *Styl*, stylet; *Tend*, tendons of sternum IX and phallosome.

(*MS. received for publication* 24. I. 1941.—Ed.)

THE MUSCULATURE AND NERVOUS SYSTEM OF THE PLEROCERCOID LARVA OF *DIBOTHRIORHYNCHUS GROSSUM* (RUD.)

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(With 35 Figures in the Text)

The specimens of the larva of *Dibothriorhynchus grossum* (Rud.) used in the present study were obtained from the coelom of *Gadus virens* L. caught in the deep-sea fishing grounds to the west of Ireland. The writer is indebted to Mr Jack Llewellyn of this department for the collection of the material during excursions to these fishing grounds in August 1938 and July 1939.

Dibothriorhynchus grossum was first named by Rudolphi (1819) from *Lamna cornubica*. The same species was later described by van Beneden (1850) as *Tetrarhynchus linguatula*, and by Diesing in 1854 as *Dibothriorhynchus linguatula*, the latter author used the generic name given to the species by Blainville (1828). A further synonym for the genus was *Tetrantaris* by Templeton in 1936. Lonnberg (1889) described the plerocercoid larva under the name of *Coenomorphus linguatula* (van Ben.). He created a new generic name for the species, which disappears in favour of Blainville's *Dibothriorhynchus*. The larva has also been recorded by Joyeux & Baer (1936) from several fishes in French waters though they state that its occurrence is rare. The description given by Lonnberg is in many respects brief, leaving much to be completed in the details of the musculature and nervous system. These systems therefore are described in the present paper. The proboscides, being themselves partly muscular and being so intimately connected with the musculature of the scolex, are also described.

The worms were fixed immediately on removal from the host in Gilson's fluid and later stored in 70% alcohol in which condition they were handed to the writer. Details of the musculature and nervous system have been worked out from serial sections cut transversely and longitudinally both in the facial and tangential planes. Sections were cut from 5 to 8μ and stained with Delafield's haematoxylin and eosin, orange G, or picro-indigo carmine, all of which gave good results for muscles and also for nerves. Sections stained with methyl blue eosin did not give better results. Owing to the somewhat oblique disposition of the proboscides it was difficult to examine them from sections only and so the entire proboscis was dissected out from the scolex with needles under a binocular microscope.

The larvae found measured 30 mm. in length with a maximum breadth of 5 mm. They are elongated, slightly flattened dorso-ventrally and possess a scolex like that of the adult. This measures on an average 8 mm. in length,

5 mm. in breadth at its base, and is provided with a dorsal and ventral bothridium (Fig. 26). The bothridia are deep elongated grooves extending to about half the length of the scolex and each is bordered by a prominent lip on its lateral and posterior borders but is free in front. Within the cavity of each bothridium, arising from the floor, is a median longitudinal ridge which seems to be constant in position. The four proboscides when fully evaginated do not project far beyond the surface but appear as spherical hooked knobs situated two in front of each bothridium.

Proboscides

Each proboscis consists of a muscular bulb, a proboscis sheath, and an armed protrusible proboscis provided with a retractor muscle (Fig. 1). The proboscis sheath is further divided into two distinct regions, an anterior wider portion into which the proboscis can be withdrawn and which contains the retractor muscle, and a posterior narrower portion with no retractor muscle. Within the proboscis sheath at its anterior end is another or anterior proboscis muscle and connected with the outside are certain extrinsic muscles which will be referred to later.

Proboscis bulb. The proboscis bulbs constitute the terminal posterior portions of the proboscides. Each is shaped rather like a banana (Fig. 1) and measures 4·5 mm. in length and is oval in transverse section with a diameter of 0·73 × 0·5 mm. (Fig. 14). The four lie slightly obliquely occupying most of the central region of the posterior half of the scolex (Figs. 23, 29). The wall of the bulb consists of three layers, an outer double cuticular layer which is continuous with the wall of the sheath, an inner layer of flattened epithelial cells lining the cavity and continuous with a similar layer in the sheath, and an intermediate layer of muscles comprising the bulk of the wall (Fig. 14). The muscular portion is not of uniform thickness, it consists of a very large number of lamellae none of which completely surrounds the lumen. On the outer convex side of the bulb which is that nearer the surface of the scolex the wall consists only of the cuticular outer wall and epithelial lining. The cuticle here is thickened to form the points of origin and insertion of the muscle fibres of the intermediate layer which are arranged in two oblique series crossing one another. The fibres have not been found to be striated as was stated by Lonnberg (1889). Several other authors have described a so-called striation in these muscle fibres in various Tetrarhynchs. Pintner (1880, 1893) stated that there are transversely striated fibres in the proboscis bulbs of *Tetrarhynchus longicollis* van Ben. and *T. smaridum* Pintner. Vaullegeard (1889), too, described striated fibres in the bulbs of *T. rufficollis* Eisenhardt. Johnstone (1911) found that in *Grillotia erinacea* (van Ben.) no such striation occurs but there is a close interlacing of the fibres which gives an appearance of striation which probably occurs also in other species and which led previous authors to regard what is really an artefact as a true transverse striation. The lumen of the bulb is towards the outside, its diameter being about equal to half that of

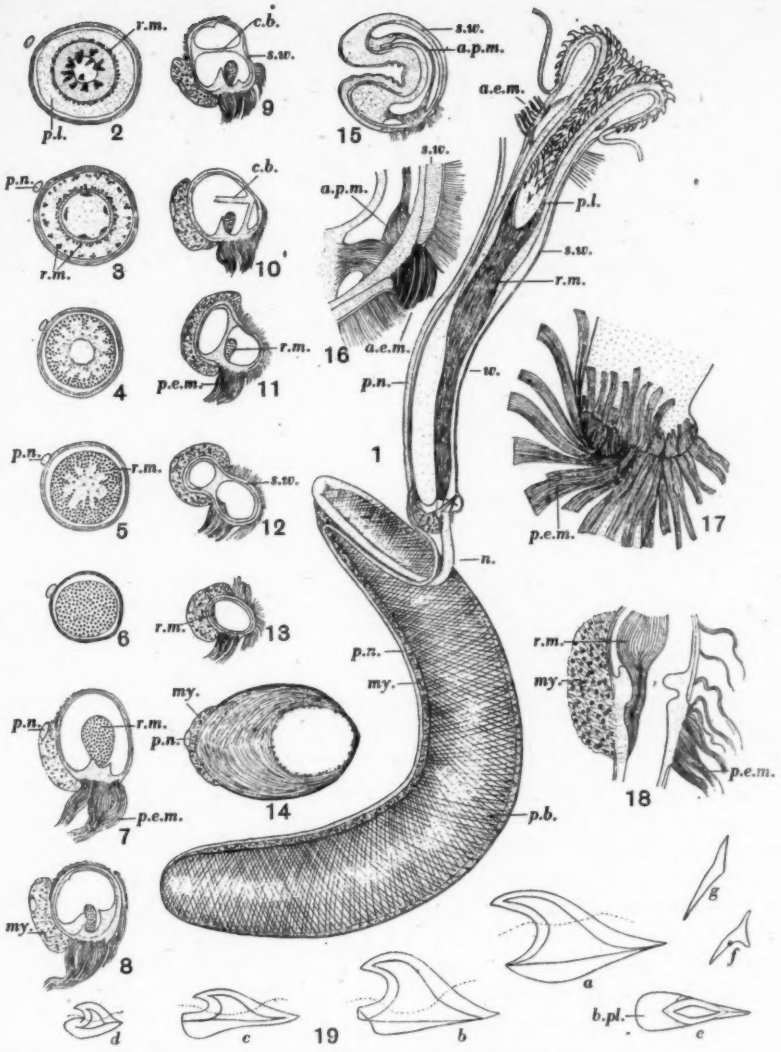

Fig. 1. Entire proboscis removed from scolex together with proboscis nerve.

Figs. 2–6. A series of transverse sections passing backwards through the anterior wider region of the proboscis sheath.

Figs. 7–13. A series of transverse sections through the posterior end of the wider region of the proboscis sheath, near its junction with the narrow region.

Fig. 14. Transverse section through proboscis bulb.

Fig. 15. Transverse section through opening of proboscis showing anterior proboscis muscle.

Fig. 16. Portion of Fig. 15 showing origin of anterior proboscis muscle and insertion of anterior extrinsic muscles.

Fig. 17. Posterior extrinsic muscles inserted on to junction between wide and narrow regions of proboscis sheath.

Fig. 18. Longitudinal section of the same region showing origin of proboscis retractor from inner wall of proboscis sheath.

Fig. 19. Proboscis hooks, and a series from the apex down the outside of the evaginated proboscis to its base; *e*, surface view of hook; *c*, *f* and *g*, simple hooks from base of invaginated portion.

the bulb (Fig. 14). On the median side, that is along the concave border, lies a band of cells (Figs. 1, 14, 29) which have a structure similar to myoblasts and may play some part in forming new muscle lamellae. This seems very possible as they are closely connected with the muscle fibres, the cuticular wall being absent along the line of contact (Fig. 14). The lumen contains fluid only; what Lonnberg refers to as a retractor muscle is probably the fluid which coagulates on fixation into a mass in the centre. Contraction of the muscle bulb exerts pressure on the contained fluid which is communicated in turn to the proboscis sheath and so evaginates the proboscis.

Proboscis sheath. The anterior region of the proboscis sheath is wider than, and about twice as long as, the posterior region (Fig. 1). It measures 3·53 mm. in length and 0·4 mm. in breadth. The diameter of the posterior region is 0·095 mm. At the junction between the two is a bulb-like dilatation for the insertion of the posterior extrinsic muscles. The wall of the sheath is cuticular, continuous with that covering the bulb and consists of two layers throughout. The thickness of the wall varies in different parts of the sheath. In the narrow posterior region it is very thin, but at the point of junction between the two regions it is thicker than anywhere else, probably to provide support for the insertion of the extrinsic muscles on the outside and the origin of the retractor on the inside (Figs. 7–13, 18). The cavity here, too, is traversed by cuticular projections and bars, the arrangement of which is illustrated in Figs. 7–12. The retractor muscle at its origin is bounded on either side by a longitudinal fold of cuticle which projects into the lumen of the sheath (Figs. 7–10, 18). These folds lie at the extreme posterior end of the wider portion of the sheath. One of these (Figs. 10–12) becomes continuous posteriorly with the rim surrounding the opening into the narrow posterior portion of the sheath. The second cavity which appears on the left-hand side in Figs. 11 and 12 is merely the bulb-like posterior extremity of the wide portion which has disappeared in the section next behind (Fig. 13). Shortly before the opening into the narrow region two cuticular bars traverse the cavity of the sheath completely. One of these passes dorso-ventrally (Figs. 9, 10) and the other obliquely and laterally across one corner (Fig. 10). These bars form a framework which serves as an additional support to counteract the pull of the contracting muscles.

The extrinsic muscles of this region are inserted on to the side of the sheath nearest the surface of the body (Figs. 23, 29). Associated with them in each proboscis is a mass of cells similar to those connected with the proboscis bulb; they form a 'cushion' at the posterior extremity of the wide region of the sheath (Figs. 1, 7–13, 17, 18), terminating opposite the posterior limit of the origin of the retractor muscle.

The wall of the proboscis sheath here, as elsewhere, is made up of two layers each consisting of very fine diagonal fibres. At the point of insertion of the extrinsic muscles the outer layer has a frayed appearance, the muscles passing into the wall for a short distance (Figs. 7–13). After the retractor muscle leaves the wall of the sheath the latter becomes at once quite thin (Figs. 2–6) and

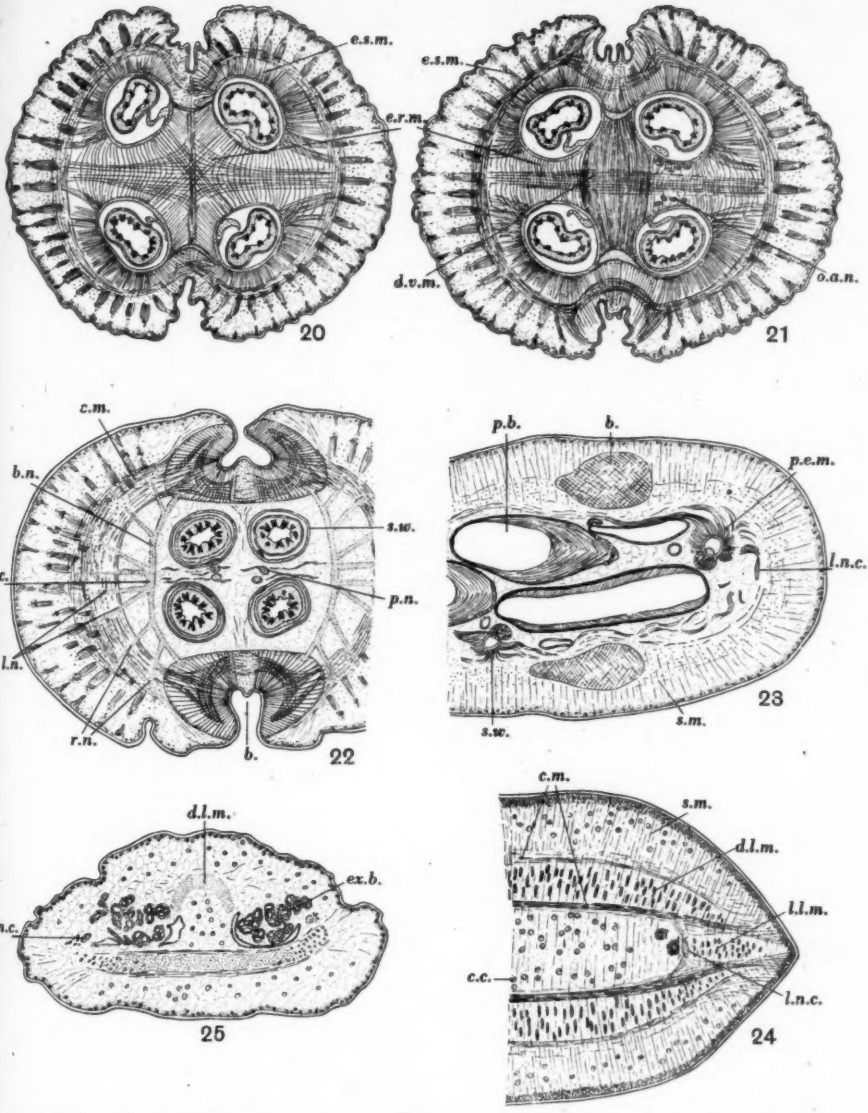

Fig. 20. Transverse section through anterior extremity of scolex showing extrinsic radiating muscles and extrinsic sagittal muscles.

Fig. 21. Transverse section through anterior extremity of scolex showing dorso-ventral muscle mass.

Fig. 22. Transverse section of scolex through median region of bothridia showing origin of bothridial nerves and lateral nerves from the lateral nerve cords.

Fig. 23. Transverse section through posterior region of scolex showing oblique arrangement of proboscis bulbs, and posterior extrinsic muscles of proboscis sheath.

Fig. 24. Transverse section through body showing arrangement of musculature.

Fig. 25. Transverse section through posterior extremity showing excretory bladder and arrangement of muscles.

remains so until at about one-third of the way from the anterior extremity when it gradually thickens a little to the point where it is attached to the body wall (Fig. 15).

Proboscis. The surface layer of the protrusible proboscis is continuous with the cuticle covering the scolex (Fig. 1). It becomes gradually thinner as it passes down to the narrow base of the invaginated portion. In this layer are embedded the proboscis hooks which are arranged in a series of alternating rings around the proboscis. All the hooks of the protrusible part are essentially similar in structure but vary in size. When the proboscis is fully evaginated the largest hooks (Fig. 19 *a*) are at the apex. The individual hooks of each ring are the same size, but members of successive rings gradually decrease in size down the outer side of the proboscis until those at the base are very small (Fig. 19 *b–d*). Due probably to the spherical nature of the proboscides these latter never function. Each hook consists of a triangular basal plate which is embedded in the cuticle, the base of the triangle being posterior (Fig. 19 *e*) and a hooked spine which, in the evaginated state, is directed backwards. The deepest portion of the proboscis is never evaginated but this, too, is armed (Figs. 1, 3). The hooks of the non-evaginable portion are sparsely distributed and of very simple structure, being elongated spines with no basal plate (Fig. 19 *f*, *g*). The apices of these always project backwards whereas the apices of those previously mentioned project forwards in the invaginated proboscis, so that they may come to point backwards in the evaginated condition.

Retractor muscle of proboscis. As already mentioned, the proboscis retractor muscle originates at the junction of the wide and narrow regions of the sheath and from the side towards the centre of the scolex (Figs. 1, 18, 23). Opposite to its origin on the outside of the wall of the sheath is the mass of myoblasts from which connecting strands of protoplasm pass through the wall to the base of the retractor (Fig. 18). The retractor muscle soon separates from the wall and passes forwards through the lumen of the sheath (Figs. 1, 6). Near the base of the invaginated proboscis the muscle fibres become concentrated peripherally, leaving a protoplasmic tissue containing nuclei in the centre (Fig. 5). This latter surrounds the narrow base of the proboscis (Fig. 4). The muscle fibres become inserted on to the proboscis wall in rings, some more posteriorly and others a little further forwards (Fig. 3). They traverse the protoplasmic tissue which they formerly surrounded and continue along the wall of the proboscis for a short distance (Fig. 2). The protoplasmic tissue now forms a layer surrounding the proboscis proper, this is wide posteriorly (Figs. 1, 2), but gradually narrows anteriorly (Figs. 1, 15, 20–22) extending as far as the junction of the proboscis with the body wall and sheath.

Anterior proboscis muscle. This muscle originates from the anterior extremity of the proboscis sheath on its inner side, sending a branch round on each side of the proboscis so as almost to encircle it (Figs. 1, 15, 16). The fibres of this muscle are inserted into the protoplasmic layer which lines the cuticular covering of the proboscis. Possibly it acts as a sphincter closing the aperture

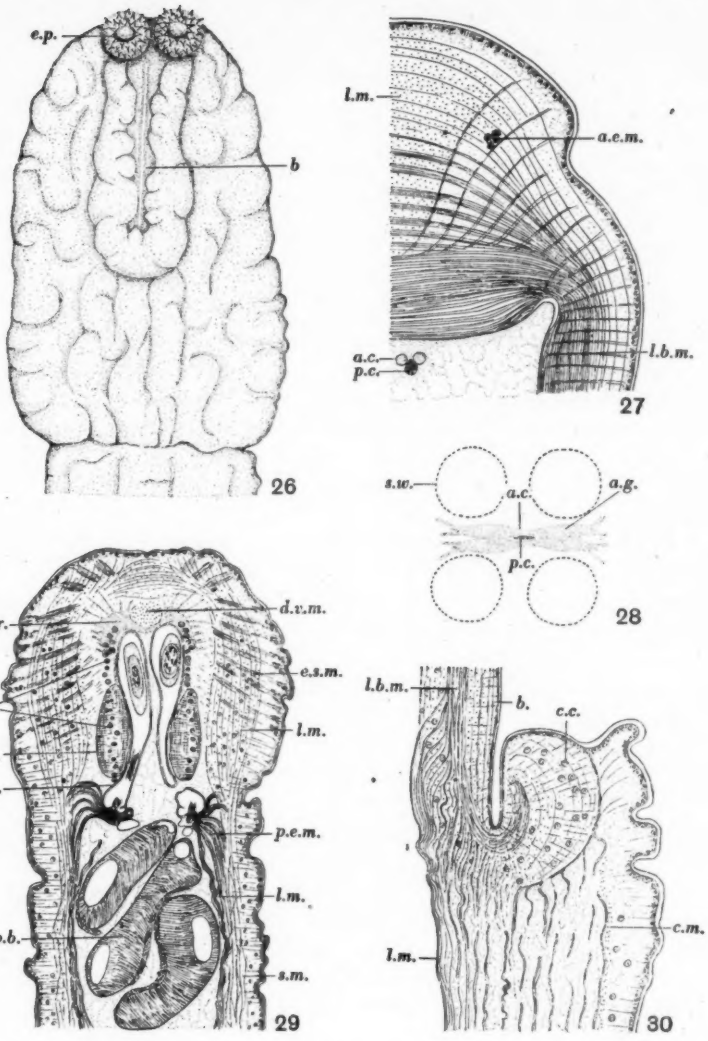

Fig. 26. Scolex of plerocercoid larva, dorsal view.

Fig. 27. Tangential longitudinal section through half of the anterior extremity of the scolex showing the longitudinal muscles emerging from the bothridium.

Fig. 28. Transverse section through brain and commissures.

Fig. 29. Facial longitudinal section through scolex showing bothridial nerves in section, musculature of scolex, and posterior extrinsic muscles of proboscides.

Fig. 30. Tangential longitudinal section through posterior end of bothridium showing entry of longitudinal muscles.

when the proboscis is withdrawn. Opposite its point of origin and on the outside of the sheath is another set of extrinsic muscles, the anterior extrinsic muscles (Figs. 1, 15, 16), which will be referred to later.

Musculature

Muscles of body. Two layers of transverse muscles and one of longitudinal run without interruption continuously throughout the body (Fig. 24). The transverse muscles are arranged in outer and inner layers with the longitudinal muscles between them. The outer layer is thinner, looser, and more delicate than the inner. The transverse muscles do not form a complete ring, but laterally the fibres of both inner and outer layers spread out, anastomose slightly with one another and end in brush-like extremities near the lateral surface. A few of the fibres from the inner layer pass dorso-ventrally in the neighbourhood of the lateral nerve cord and possibly these act in some way as a support for the cord. The longitudinal muscles are arranged in bundles several layers deep and are elongated in the sagittal plane. They are not continuous, and laterally there is a gap in which lies a separate band of longitudinal muscles which appears oval or wedge-shaped in transverse section. These extend from the lateral nerve cord to the lateral margin of the body, the bundles being elongated dorso-ventrally. In longitudinal section an anastomosis is apparent between constituent fibres of adjacent bundles (Fig. 29).

In the parenchyma outside the transverse muscles are the sagittal muscles which are fine, delicate, single fibres, extending dorsally and ventrally (Fig. 24). At the lateral margins of the body the sagittal muscles become dorso-ventral muscles extending across the lateral edge from the dorsal to the ventral sides.

In addition to these more deeply seated muscles, there is a layer of longitudinal fibres situated below the cuticle and basement membrane (Fig. 24).

The arrangememt of muscles described above is constant throughout the body except for the extreme posterior end where it is modified slightly. Here is situated the complicated excretory bladder opening by a terminal pore. On the dorsal side, the outer and inner transverse muscles disappear near the early part of the bladder, leaving only the longitudinal muscles (Fig. 25) which form a curved band dorsally consisting, as does the ventral band, of isolated fibres which are no longer arranged in bundles.

Muscles of the scolex. (1) *Longitudinal muscles.* The longitudinal muscles passing dorsally and ventrally throughout the body extend forwards into the scolex. In the mid-dorsal and mid-ventral lines they pass straight into the bothridia (Figs. 22, 23, 30). Their arrangement within the bothridia will be described later. Anteriorly, the longitudinal muscles emerge from the bothridia, the dorsal and ventral fibres becoming continuous across the extreme anterior region of the scolex (Fig. 27). At the lateral margins of the body, that is from the limit of the dorsal round to the ventral bothridium on each side, the longitudinal muscles separate into two layers, an inner and an outer. The inner forms the posterior extrinsic muscles of the proboscides to be referred to later,

and the outer continues forwards through the scolex, the bundles separating into fibres which spread out so as to occupy a much wider area than they did previously (Fig. 29). They pass to the apex of the scolex where they cross over, the fibres of both sides becoming continuous. At the anterior extremity of the scolex there is therefore a mass of muscles formed from the dorsal and ventral and the lateral longitudinal fibres which cross one another at right angles.

(2) *Circular muscles.* The circular, or transverse muscles, are well defined in the body, but in the scolex are less distinct, being hardly recognizable in the region around the proboscis bulbs (Fig. 23). Further forwards they are again apparent, forming a fairly broad band of delicate fibres running round each side of the body, becoming continuous with the circular muscles within the bothridia (Fig. 22). The circular fibres persist almost to the tip of the scolex forming in front of the ill-defined anterior margins of the bothridia a complete circle (Figs. 20, 21). The longitudinal and circular fibres in the scolex are interspersed with one another and not separated into distinct layers as in the body.

(3) *Sagittal muscles.* In the body the sagittal muscles are single delicate fibres (Fig. 24), but in the scolex they become extremely well developed, forming the most prominent part of the musculature. They begin to thicken at a level about half way along the length of the proboscis sheath (Fig. 29), they pass obliquely backwards so that the whole muscle does not appear in a single transverse section (Figs. 20–22). They are not restricted to the dorsal and ventral sides as in the body, but may be more correctly termed radial muscles as they radiate out in all directions, being absent only in the regions occupied by the bothridia. Near the surface they terminate in brush-like extremities surrounded by cells (Figs. 20–22). The inner ends of those nearest the proboscis sheaths are inserted on to them and will be referred to later as the extrinsic sagittal muscles, while those situated at the lateral margins of the scolex are continuous with those of the opposite side right across the substance of the scolex (Figs. 20, 21).

Muscles of bothridia. The bothridia are not very sharply demarcated from the underlying tissues especially towards their anterior ends. Running through the centre of each bothridium occupying its whole depth is a band of longitudinal muscles continuous with those of the body (Figs. 22, 27, 30). In addition, there is a layer of longitudinal fibres lying below the cuticle lining the cavity of the bothridium and also along its inner border (Fig. 22). These outer and inner longitudinal muscles are continuous with one another around the posterior margin of the sucker (Fig. 30), while anteriorly they pass out with the main mass of muscles into the anterior region of the scolex. The circular muscles form a band parallel to the cavity of the bothridium lying about half way along its depth. In the central region the fibres spread out and are intermingled with the longitudinal muscles; laterally, some of them become continuous with the circular muscles of the scolex (Fig. 22). The radial muscles

of the bothridia are in the form of delicate fibres which radiate out through the depth of the sucker (Fig. 22). They are not present in the central region occupied by the band of longitudinal muscles.

Extrinsic muscles of the proboscides. (1) *Posterior extrinsic muscles.* As already mentioned, these originate from the inner layer of longitudinal muscles at the lateral margins about half way along the length of the scolex (Fig. 29). They pass inwards and become inserted on to the wall of the proboscis sheath at the junction between the wide and narrow regions (Figs. 1, 7–13, 17, 18, 23, 29). They form strong bands of muscles (Fig. 17) whose function is probably to hold the proboscis in position during the contraction of the muscular bulb and of the retractor muscle. Associated with these muscles, as already mentioned, is the cushion-shaped mass of myoblasts.

(2) *Anterior dorso-ventral muscles.* Near the anterior end of the scolex and just in front of the brain (Figs. 21, 27, 29) is a spindle-shaped mass of muscle fibres. These have their origins and insertions on a narrow sheet of cuticular material which passes across dorsally and ventrally, connecting the two dorsal and two ventral proboscis sheaths (Fig. 21) and being continuous with the substance of their walls. Contraction of this mass of muscles together with the contraction of the muscles of the scolex in this region may help in the evagination of the proboscides.

(3) *Extrinsic sagittal muscles.* Towards the anterior end of the scolex the dorso-lateral and ventro-lateral sagittal muscles on each side are inserted on to the proboscis sheaths (Figs. 20, 21).

(4) *Extrinsic radiating muscles.* The radiating extrinsic muscles are first apparent just in front of the brain, here they extend in a dorso-ventral direction connecting the two dorsal with the two ventral proboscis sheaths, on either side of the anterior dorso-ventral muscles (Fig. 21). In front of this region fibres radiate from the sheaths on all sides (Fig. 20). Those on the outside are, as previously stated, continuous with the sagittal muscles of the scolex, the remainder are distributed as follows: the two dorsal proboscis sheaths are connected together and the two ventral, each dorsal sheath is also connected to the ventral sheath of the same side by dorso-ventral fibres, and to the ventral of the opposite side by diagonal fibres. This region of the scolex, therefore, possesses an elaborate arrangement of muscles, the contraction of which probably results in an increase in the diameter of the proboscis sheath which will facilitate invagination of the proboscis.

(5) *Anterior extrinsic muscles.* There is one other set of extrinsic muscles connected with the proboscis sheaths. These originate from and are inserted on the proboscis sheath opposite the point from which the anterior proboscis muscle originates on the inside (Figs. 1, 15, 16). It consists of only a few bundles of fibres which extend between the two dorsal and two ventral proboscis sheaths (Fig. 27). Their function is probably concerned with opening and closing the aperture of the invaginated proboscis.

NERVOUS SYSTEM

The nervous system is better defined than in many cestodes, due possibly to the large size of the scolex in this species. It consists of a brain, two lateral nerve cords and nerves supplying various parts of the body. These latter may

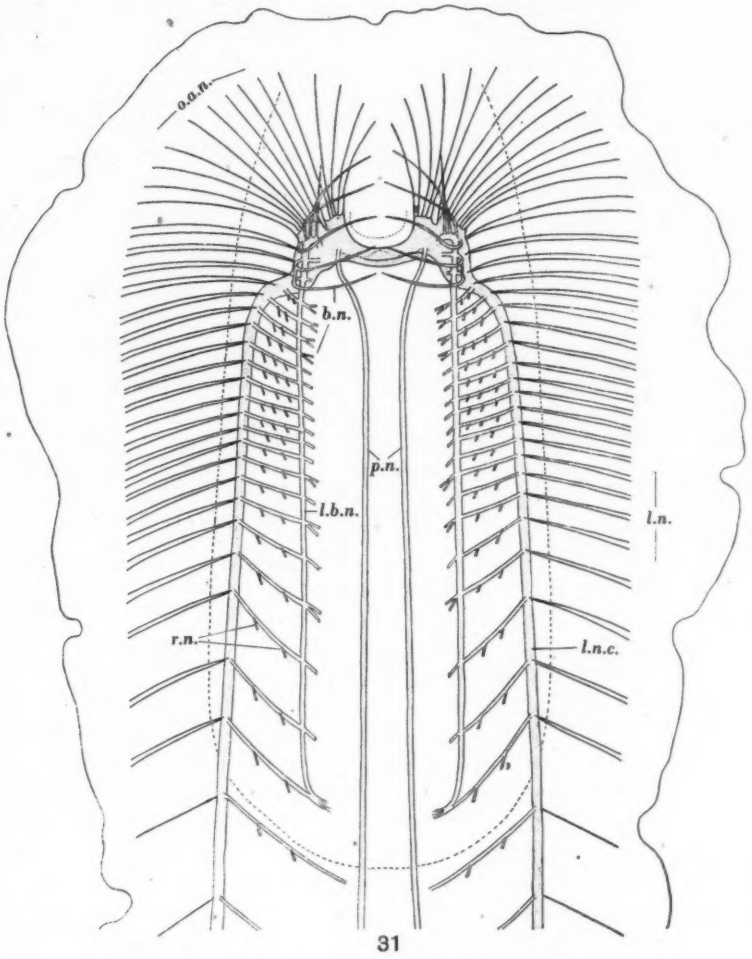

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Fig. 31. Dorsal half of nervous system of anterior end of scolex.

be arranged under the following headings: anterior nerves supplying the anterior regions of the scolex, bothridial nerves supplying the bothridia, branches from the lateral nerve cords to the surface regions of the body, and proboscis nerves to the proboscides.

Brain. The brain (Fig. 33) is situated near the anterior end of the scolex (Fig. 29), immediately behind the dorso-ventral muscle mass. It is elongated laterally, and compressed dorso-ventrally, owing to the presence of bothridia and proboscides (Fig. 28). It consists of paired masses, which for convenience will be called ganglia, of which there are two right and two left dorsal, and two right and two left ventral, one pair anterior and the other pair posterior (Fig. 33). The anterior ganglia are better defined than the posterior, they form a rounded mass on each side dorsally and ventrally, the two dorsal and the two ventral being connected by transverse anterior commissures which pass parallel to one another, close together, across the middle of the scolex (Figs. 28, 33). The dorsal and ventral ganglia of each side fuse together at their posterior borders (Figs. 32–34) and from the points of fusion another commissure arises, the posterior median commissure, which runs parallel to, and slightly behind, the anterior commissures (Figs. 33, 34). Laterally, at its point of origin the median commissure is small in diameter (Fig. 34), but as it approaches the centre of the scolex its diameter increases until it is greater than that of the anterior commissures and is pear-shaped in transverse section (Fig. 35). In the centre of the scolex the three commissures are quite separate from one another, the median projecting upwards for a slight distance between the two anterior (Figs. 28, 33).

The anterior ganglia become continuous behind with the posterior ganglia which are not as well defined and are really the enlarged commencements of the lateral nerve cords (Fig. 33). On their outer borders they are free from one another, while internally they are fused, the fusion being continuous with that of the internal borders of the anterior ganglia.

The terms ganglia and commissures are not strictly correct, but are retained temporarily, as are the same terms by Johnstone (1911) for *Grillotia erinacea* (van Ben.). Ganglia should contain nerve cells, and the commissures, fibres, or processes from the nerve cells. Here, however, the so-called ganglia consist of a tissue resembling parenchyma and which seems to be composed of a network of fine fibres enclosing small spaces containing a few nuclei. The posterior median commissure is the only part of the nervous system in which ganglion cells have been found to occur (Figs. 28, 34, 35). This therefore is the true nerve centre. Pintner (1880) found a somewhat similar arrangement in *Tetrarhynchus*

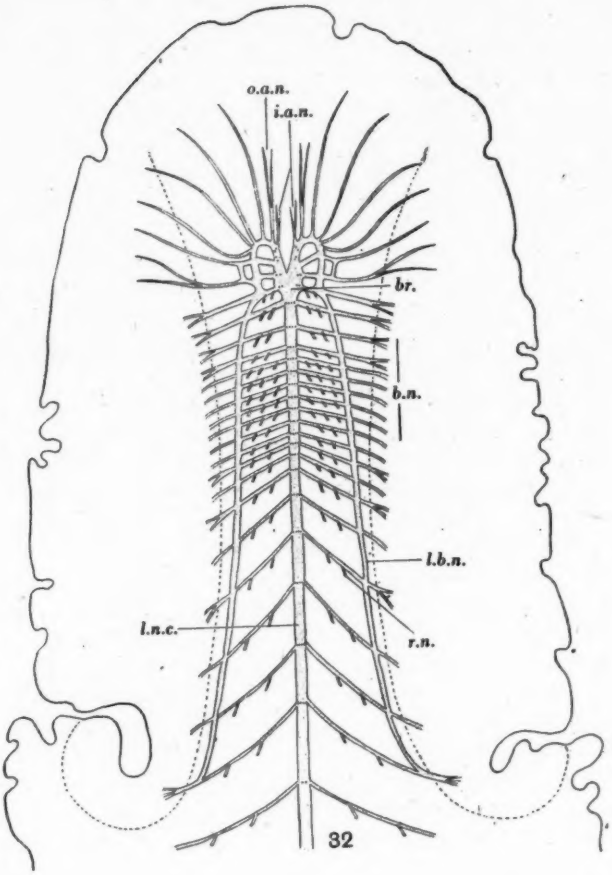
Legends to Figs. 32–35

Fig. 32. Lateral view of brain, and lateral nerve cords, giving off dorsal and ventral bothridial nerves. The points of origin of the lateral nerves are indicated on the nerve cord by dots.

Fig. 33. Brain: the right side shows a dorsal view of the brain and nerves arising from it, on the left side the dorsal outer and inner anterior nerves are omitted in order to show an inside view of the ventral inner and outer anterior nerves.

Fig. 34. Transverse section of brain showing origin of dorsal and ventral anterior nerves, and proboscis nerves.

Fig. 35. Transverse section through the central region of the two anterior and the median posterior commissures.



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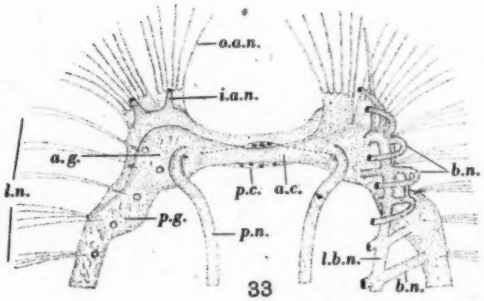

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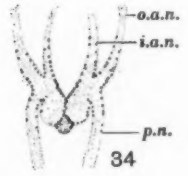

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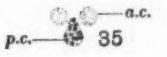

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Figs. 32–35.

longicollis van Ben., where, instead of a median posterior commissure, he describes a ganglionic mass occupying a similar position and the so-called ganglia are represented as fibrous in structure. The same condition is also seen in *Grillotia erinacea* (van Ben.) described by Johnstone (1911), who suggests that in general terms the brain might be described as a ganglionic centre surrounded by a ring-shaped commissure.

The ganglia and commissures are bounded by a delicate limiting layer which contains a number of nuclei especially around the roots of the nerves (Fig. 34).

Lateral nerve cords. The lateral nerve cords extend throughout the whole length of the body one on either side. From their origins and during their course through the scolex they pass obliquely outwards (Fig. 31), while in the body they pursue a straight course to the posterior extremity. The double nature of the cord is apparent in the scolex, but in the body it becomes uniformly oval in transverse section (Fig. 24). It is situated midway between the dorsal and ventral surfaces and just inside the lateral group of longitudinal muscles.

Anterior nerves. The anterior nerves supply the anterior extremity of the scolex. They arise from the frontal margins of the anterior ganglia, there being an outer and an inner from each of the four (Figs. 31–34).

(1) *Outer anterior nerves.* The outer dorsal and ventral anterior nerves arise from each ganglion by two broad roots situated close together (Fig. 33). Shortly after its origin each divides into a number of nerves which spread out fanwise. Each nerve also divides into two in such a way that the 'fan' is double (Fig. 32). There is therefore a dorsal and ventral double fan-shaped set of nerves proceeding anteriorly and antero-laterally to supply the anterior and antero-lateral borders of the scolex (Figs. 29, 31).

(2) *Inner anterior nerves.* Immediately within the outer anterior nerves and arising at the same point are the inner anterior nerves, two on each side dorsally and ventrally (Figs. 32–34). They are parallel with the outer but are very much smaller, and they, too, divide to form a double 'fan' (Fig. 32) which is less extensive than in the case of the outer nerves. They are shorter and supply only the deeper regions of the scolex and muscles of the proboscis sheaths.

Bothridial nerves. The bothridia, being much elongated, have an extensive nerve supply, each being provided with twenty-five pairs of nerves more or less evenly distributed along its length (Fig. 31). The anterior seven pairs of nerves arise by four roots from the brain both dorsally and ventrally, and the remaining eighteen from the lateral nerve cords on either side. Before the bothridial nerves enter the bothridia they are joined together by a longitudinal bothridial nerve; there are four of these latter, one on either side of the inner margin of each bothridium. The first four bothridial nerves correspond to one root which arises from the anterior ganglion just behind the more lateral of the outer anterior nerves (Fig. 33). The fifth bothridial nerve corresponds to the second root which arises shortly behind and a little to the inside of the

first. The third and fourth roots, belonging to the sixth and seventh nerves respectively, arise from the posterior ganglion. Shortly after their origin these four roots are connected together by what is the commencement of the longitudinal bothridial nerve (Figs. 31–33), and the fifth and sixth nerves are further connected by a short longitudinal bar. The dorsal bothridial nerves curve round dorsally, and the ventral ones ventrally, to supply the anterior portion of each bothridium (Figs. 31–32). The remaining eighteen pairs of bothridial nerves arise from the lateral nerve cords on either side each by its own root (Figs. 31–32). These nerves curve outwards in an arc on either side, each bothridium therefore being supplied with two series, one on each internal lateral border (Fig. 22). The first twelve pairs which lie in the region of the proboscis sheaths are situated fairly close together, while the remaining six, which are opposite the proboscis bulbs, are more widely separated and take a slightly oblique course backwards before entering the bothridia (Figs. 31, 32). Within the bothridia some of the nerves have been found to divide (Figs. 31, 32), but the branching could not be traced for all of them. The four longitudinal bothridial nerves pass obliquely outwards from their commencement near the brain until they come to lie close to the margins of the bothridia on each side just at the point where the bothridial nerves enter. They connect all the bothridial nerves together, giving the nervous system a ladder-like appearance in this region. Possibly they act as a support for the bothridial nerves during the contraction of the bothridial and scolex muscles, or the invagination or evagination of the proboscides. During its course from the lateral nerve cord to the bothridium each bothridial nerve from the seventh to the twenty-fifth gives off two or three radial nerves which extend dorso- and ventro-laterally outwards, and obliquely backwards, to supply the surface layers in this region (Figs. 22, 31, 32). Nerves seven to ten, and sixteen to twenty-five, give off two nerves each and nerves eleven to fifteen three nerves each.

Nerves supplying the lateral regions of the body. Nerves supplying the lateral regions arise from the brain and lateral nerve cords along their whole length. They are more abundant in the scolex than in the body, especially in the anterior half. Arising from the brain and close to each of the first four bothridial roots are two lateral nerves, the first two from the anterior ganglia, both dorsally and ventrally, and the second two from the posterior ganglia. These pass out to the lateral margins, being almost a continuation of the fan-like arrangement seen in the outer anterior nerves (Figs. 31–33). The remaining lateral nerves arise from the lateral nerve cords. A group of four is apparent on the outside of each between the origins of the bothridial nerves (Figs. 22, 31–33). The two median of these pass directly laterally towards the surface of the body, and those on either side of them slightly obliquely outwards (Fig. 22). The scolex in the neighbourhood of the bothridia is therefore abundantly supplied with nerves, there being a series of rings of nerves, one behind the other, each giving off radial and lateral nerves on the outside, supplying all the superficial parts of the scolex.

Behind the bothridia, nerves corresponding to the bothridial nerves continue to arise from the lateral nerve cords at intervals in pairs, these supply the dorsal and ventral regions previously occupied by the bothridia. They, too, give off each two radial branches to the dorso- and ventro-lateral regions (Figs. 31, 32). Corresponding to the group of four which are present between them more anteriorly there are here only two which extend outwards to the lateral margins. The groups of nerves arising from the lateral nerve cords in the body are more widely separated and more oblique in their course than are those in the scolex.

Proboscis nerves. Each proboscis is provided with a nerve running along its whole length (Fig. 1). These arise, two dorsally and two ventrally, from the anterior ganglia (Figs. 31, 33), the point of origin being adjacent to that of the more median of the outer and inner anterior nerves (Figs. 33, 34). They pass backwards through the scolex, one near to, and on the inner side of each proboscis sheath (Figs. 2, 3, 22). As they proceed backwards each nerve becomes applied to the proboscis sheath (Figs. 4–6) and at the point of junction between the wide and narrow regions it passes into the mass of myoblasts and lies near its outer margin (Figs. 1, 7–13). It then continues, parallel to the narrow region of the sheath and to the proboscis bulb to its extremity (Fig. 1) where it terminates in fine branches. During its course along the proboscis bulb the proboscis nerve lies along the inner concave border embedded near the surface of the layer of muscle cells (Fig. 14).

The nervous system has several points in common with that of *Grillotia erinacea* described by Johnstone (1911) and *Tetrarhynchus smaridum* described by Pintner (1880). It is a little more complicated, because of the much elongated bothridia and the great increase in the number of bothridial nerves.

Summary

1. The structure of the proboscides of the larva of *Dibothriorhynchus grossum* (Rud.) is described. Each proboscis is provided with four sets of extrinsic muscles, and there is an anterior dorso-ventral muscle mass connected to all four proboscides.

2. The musculature of the body and scolex is described.

3. The nervous system consists of a brain, two lateral nerve cords, two outer and inner anterior nerves on each side, twenty-five pairs of bothridial nerves to each bothridium, four longitudinal bothridial nerves connecting these latter before their entry into the bothridia, four proboscis nerves arising from the brain, and a series of lateral nerves supplying the lateral regions of the body.

4. The so-called ganglia contain no nerve cells, these are present only in the posterior median commissure which is therefore the nerve centre.

Key to Lettering of Figures

All drawings are semi-diagrammatic and in some cases have been simplified for clarity.

a.c. anterior commissure
a.e.m. anterior extrinsic muscles of proboscis
a.g. anterior ganglion.
a.p.m. anterior proboscis muscle
b. bothridium
b.l.m. longitudinal muscles of bothridium
b.n. bothridial nerve
b.pl. basal plate of hook
br. brain
c.b. cuticular bars in cavity of proboscis sheath
c.c. calcareous corpuscles
c.m. circular muscles
d.l.m. dorsal longitudinal muscles
d.v.m. dorso-ventral muscle mass
e.p. evaginated proboscis
e.r.m. extrinsic radiating muscles
e.s.m. extrinsic sagittal muscles
ex.b. excretory bladder
i.a.n. inner anterior nerve
l.b.n. longitudinal bothridial nerve
l.l.m. lateral longitudinal muscles
l.m. longitudinal muscles
l.n. lateral nerves
l.n.c. lateral nerve cord
my. myoblasts
n. posterior narrow portion of proboscis sheath
o.a.n. outer anterior nerve
p.b. proboscis bulb
p.c. posterior commissure
p.e.m. posterior extrinsic muscles
p.g. posterior ganglion
p.n. proboscis nerve
p.l. protoplasmic layer of proboscis wall
r.m. retractor muscle of proboscis
r.n. radial nerve
s.m. sagittal muscles
s.w. wall of proboscis sheath
w. anterior wide portion of proboscis sheath

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A RECORD OF THE TREMATODE AND CESTODE PARASITES OF FISHES FROM THE PORCUPINE BANK, IRISH ATLANTIC SLOPE AND IRISH SEA

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The trematode and cestode parasites of fishes inhabiting British coastal waters have been the subject of several studies in the past, but the parasites of deep-sea fishes have received comparatively little attention due probably to the difficulty of obtaining fresh material. In order that such material might be obtained, excursions were made by the junior author in a commercial trawler to some of the deep-sea fishing grounds lying to the west of Ireland, namely, the Irish Atlantic Slope and the Porcupine Bank. Two excursions were made, the first in August 1938 and the second in July 1939, each extending over a period of about 12 days. In addition, a study has been made of the parasites of some fishes from the Irish Sea from 1936 to 1939. The results of both surveys are incorporated in this paper, and the areas investigated are indicated in Table 1.

Table 1. *Localities from which fishes were obtained*

The numbers given to the localities in the first column are referred to in Table 3.

	Locality	Area
1	Colwyn Bay	Irish Sea (depth 0–50 fm.)
2	Aberystwyth	
3	Newquay	
4	Milford Haven	
5	54° N., 11° 10′ W.	Irish Atlantic Slope (depth 120–150 fm.)
6	53° 30′–54° N., 11° 40′ W.	
7	52° 25′ N., 12° W.	
8	52° 55′–53° 30′ N., 14° W.	Porcupine Bank (depth 160–200 fm.)

A record of the trematode parasites of British marine fishes has been compiled by Nicoll (1915), who added to his data details from other British surveys, namely, that of Scottish waters by T. Scott (1901), of the Irish Sea by A. Scott (1904) and of the Northumberland coast by Lebour (1908). He also refers to records from Ireland by Bellingham in 1844 and Southern in 1912. Nicoll's list, however, is not confined to British observations but includes records of trematodes from fishes that might be regarded as British but have been caught outside British waters. It thus includes references to observations made by Rudolphi, Monticelli, Stossich, Looss, Olsson, Odhner, and van Beneden for such areas as the Mediterranean and Arctic Seas. Since then, Little (1929) has

investigated the trematode parasites of fishes off the west coast of Ireland, Woodland (1927) the cestodes at Plymouth, and Baylis & Jones (1933) the helminth parasites from fishes in the same area. The cestode parasites of fishes around the British Isles have received less attention than the trematodes, no regional work having been done except that by Woodland, and Baylis & Jones.

Continental studies on trematodes of coastal fishes have been made by van Beneden & Hesse (1863), St Remy (1891, 1898), Goto (1894), Cerfontaine (1896, 1898, 1900), MacCallum (1913, 1916, 1917), Johnston & Tiegs (1922), Sprehn (1933), Yamaguti (1937–8), and Price (1937), and of cestodes by van Beneden (1850), Beauchamp (1905), Yoshida (1916), Southwell (1932), and Joyeux & Baer (1936).

The writers have been unable to trace any British records of the parasites of deep-sea fishes apart from brief references made by Scott (1901) and Nicoll (see Little, 1929) to parasites 'taken from deep-sea fishes landed at Aberdeen'.

The only other author who has worked on the deep water off the coast of Ireland is Gallien (1937). This field of study seemed therefore to present possibilities.

From the deep-sea fishing grounds 408 host fishes belonging to thirty-three different species were examined, and from the Irish Sea 169 belonging to sixteen species. Fishes caught by the trawler were investigated immediately, all parts of the body being examined. Those caught in the Irish Sea were sent into the laboratory at Aberystwyth for examination. Trematodes and cestodes were fixed in Gilson's fluid and stored in 70% alcohol. *In toto* preparations were stained with Ehrlich's haematoxylin.

A list of the fishes examined, together with their parasites, is given in Table 2. The names used for the hosts are those in the *British Museum List of British Vertebrates*.

Table 2. *List of host fishes with their parasites*

I.A.S.—Irish Atlantic Slope; P.B.—Porcupine Bank; I.S.—Irish Sea.

Host		Parasite
Centrophorus squamosus (Gmelin)	P.B.	*Grillotia erinacea* larva, coelom
Chimaera monstrosa L.	I.A.S.	*Discocotyle leptogaster*, gills
" "	"	*Gyrocotyle urna*, intestine
Conger conger L.	I.S.	*Prosorhynchus aculeatus*, intestine
" "	I.S. and I.A.S.	*Sterrhurus fusiformis*, stomach
" "	" "	*Lecithochirium rufoviride*, stomach
Gadus merlangus L.	I.S.	*Dactycotyle merlangi*, gills
" "	I.A.S.	*Dactycotyle minor*, gills
" "	I.S.	*Grillotia erinacea* larva, stomach wall
Gadus virens L.	I.A.S.	*Dactycotyle denticulata*, gills
" "	"	*Dibothriorhynchus grossum* larva, coelom
Glyptocephalus cynoglossus (L.)	P.B.	*Grillotia erinacea* larva, stomach wall
Hexanchus griseus (Gmelin)	"	*Squalonchocotyle grisea*, gills
" "	"	An unidentified Tetrarhynch, intestine
" "	"	*Phyllobothrium lactuca*, intestine
" "	"	*Phyllobothrium centrurum*, intestine
" "	"	*Calliobothrium verticillatum*, intestine

Table 2 (*continued*)

Host		Parasite
Limanda limanda (L.)	I.S.	*Scolex pleuronectes*, mucosa of intestine
Merluccius merluccius (L.)	P.B.	*Parabothrium bulbiferum*, intestine
,, ,,	,,	*Clestobothrium crassiceps*, intestine
,, ,,	I.A.S.	*Anthocotyle merluccii*, gills
,, ,,	,,	*Abothrium gadi*, intestine
Molva molva	I.A.S.	*Dactycotyle palmata*, gills
Pagellus centrodontus (De la Roche)	I.A.S.	*Choricotyle chrysophryi*, gills
Pleuronectis platessa L.	I.S.	*Grillotia erinacea* larva, stomach wall
Raja batis L.	P.B. and I.S.	*Echeneibothrium julievansum*, intestine
,, ,,	I.A.S. and I.S.	*Echeneibothrium variabile*, intestine
,, ,,	I.A.S.	*Acanthobothrium coronatum*, intestine
,, ,,	P.B. and I.A.S.	*Rajonchocotyle batis*, gills
,, ,,	P.B.	*Anthobothrium auriculatum*, intestine
Raja clavata L.	I.S.	*Grillotia erinacea*, intestine
Raja fullonica L.	P.B.	*Calicotyle kroyeri*, cloaca
Raja microcellata Montagu	I.A.S.	*Calicotyle kroyeri*, cloaca
Raja montagui Fowler	I.S.	*Echeneibothrium maculatum*, intestine
Raja naevus Muller & Henle	P.B.	*Calicotyle kroyeri*, cloaca
,, ,, ,,	,,	*Rajonchocotyle miraletus*, gills
,, ,, ,,	,,	*Grillotia erinacea* larva, intestine wall
,, ,, ,,	P.B. and I.A.S.	*Discobothrium fallax*, intestine
,, ,, ,,	,, ,,	*Echeneibothrium julievansum*, intestine
Raja oxyrhynchus L.	I.A.S.	*Grillotia erinacea*, intestine
Salmo trutta L.	I.S.	*Eubothrium crassum*, pyloric caeca
Scomber scombrus L.	I.A.S.	*Mazocraes scombri*, gills
Scyliorhinus caniculus (L.)	I.S.	*Acanthobothrium coronatum*, intestine
Scyliorhinus stellaris (L.)	I.S.	*Acanthobothrium coronatum*, intestine
Scymnorhinus licha (Bonnaterre)	P.B.	*Squalonchocotyle licha*, gills
Serranus cabrilla (L.)	I.A.S.	Unidentified Microcotylidae, gills
Spinax spinax (L.)	P.B.	*Aporhynchus norvegicus*, intestine
Torpedo nobiliana Bonaparte	I.S.	*Amphibdella maccallumi*, gills
,, ,, ,,	,,	*Amphibdella flavolineata*, gills
Trigla cuculus L.	I.A.S.	*Phyllocotyle gurnardi*, gills
Trigla gurnardus L.	I.A.S.	*Plectanocotyle gurnardi*, gills
Urophycis blennoides (Brunnich)	I.A.S.	*Dactycotyle phycidis*, gills

The following fishes contained no trematode or cestode parasites:

Irish Atlantic Slope: *Brosme brosme* Muller, *Gadus aeglifinis* L., *Gadus callarias* L., *Lepidorhombus whiff-iagonis* (Walbaum), *Lophius piscatorius* L., *Raja undulata* Lacapede, *Scyliorhinus caniculus* (L.), *Trachurus trachurus* L.

Porcupine Bank: *Molva byrkelange* Walbaum, *Osmerus eperlanus* L., *Trigla lyra* L.

Irish Sea: *Clupea harengus* L., *Gadus pollachius* L., *Platichthys flessus* (L.), *Solea solea* (L.), *Trigla gurnardus* L.

A classified list of the parasites, together with their hosts and the localities in which they occur, is given in Table 2. The numbers given for the different localities correspond to those in Table 1. The trematodes have been classified according to the schemes adopted by Poche in 1926 and Fuhrman in 1928 and revised by Dollfus (1937) and Southwell & Kirshner (1937). The family Diclidophoridae Fuhrman 1928 has been revised by the junior author; details of the revision will appear in a later paper. The one member found belonging to the family is here placed in the new family Choricotylidae. The cestodes have been classified from the monograph by Joyeux & Baer (1936).

Table 3. *List of parasites with their hosts*

TREMATODA

MONOGENEA

Parasite	Host	Locality	Date
GYRODACTYLIDAE van Beneden & Hesse			
Amphibdella maccallumi Johnston & Tiegs	*Torpedo nobiliana*	1	6. ix. 38
**Amphibdella flavolineatus* MacCallum	*Torpedo nobiliana*	1	6. ix. 38
MONOCOTYLIDAE Taschenberg			
Calicotyle kroyeri Diesing	*Raja montagui*	3	10. iii. 37
" " "	*Raja oxyrhynchus*	5	5. viii. 38
" " "	*Raja naevus*	6	8. viii. 38
" " "	*Raja fullonica*	6	8. viii. 38
" " "	*Raja microcellata*	6	13. vii. 39
ONCHOCOTYLIDAE Dollfus			
Rajonchocotyle miraletus sp.nov.	*Raja naevus*	8	8. viii. 38
Rajonchocotyle batis Cerf.	*Raja batis*	8	9. viii. 38
" " "	" "	6	10. vii. 39
Squalonchocotyle licha sp.nov.	*Scymnorhinus licha*	8	8. viii. 38
Squalonchocotyle grisea Cerf.	*Hexanchus griseus*	8	9. viii. 38
CHORICOTYLIDAE fam.nov.			
Choricotyle chrysophryi van Ben. & Hesse	*Pagellus centrodontus*	5	5. viii. 38
" " "	" "	7	6. vii. 39
MAZOCRIIDAE Southwell & Kirshner			
Dactycotyle minor (Olsson)	*Gadus merlangus*	5	5. viii. 38
Dactycotyle denticulata (Olsson)	*Gadus virens*	5	6. viii. 38
" " "	" "	6	9. vii. 39
Dactycotyle palmata (Leuckart)	*Molva molva*	6	11. vii. 39
Dactycotyle phycidis Parona & Perugia	*Urophycis blennoides*	6	9. vii. 39
Dactycotyle merlangi Nordmann	*Gadus merlangus*	2	7. xi. 38
Mazocraes scombri (Kuhn)	*Scomber scombrus*	6	8. vii. 39
Anthocotyle merluccii van Ben. & Hesse	*Merluccius merluccius*	6	"
Discocotyle leptogaster (Leuckart)	*Chimaera monstrosa*	6	10. vii. 39
Plectanocotyle gurnardi van Ben. & Hesse	*Trigla gurnardus*	6	"
" " "	*Trigla cuculus*	6	11. vii. 39
MICROCOTYLIDAE Taschenberg			
Unidentified species	*Serranus cabrilla*	6	12. vii. 39

DIGENEA

GASTEROSTOMIDAE Braun			
Prosorhynchus aculeatus (Odhner)	*Conger conger*	4	10. vii. 39
HEMIURIDAE Lühe			
Sterrhurus fusiformis (Lühe)	*Conger conger*	6	10. vii. 39
Lecithochirium rufoviride (Rud.)	*Conger conger*	6	"

CESTODA

CESTODARIA

Gyrocotyle urna (Grube & Wagener)	*Chimaera monstrosa*	6	11. vii. 39

EUCESTODA

TETRARHYNCHIDEA			
APORHYNCHIDAE Poche			
Aporhynchus norvegicus (Olsson)	*Spinax spinax*	8	10. viii. 38
EUTETRARHYNCHIDAE Guiart			
Grillotia erinacea (van Ben.), adult	*Raja clavata*	3	20. xi. 36
" " "	*Raja oxyrhyncha*	5	5. viii. 38
Grillotia erinacea, larva	*Gadus merlangus*	3	1936–37
" " "	*Limanda limanda*	3	"
" " "	*Pleuronectis platessa*	3	"
" " "	*Raja naevus*	8	7. viii. 38
" " "	*Centrophorus squamosus*	8	9. viii. 38
" " "	*Glyptocephalus cynoglossus*	8	10. viii. 38
An unidentified Tetrarhynch	*Hexanchus griseus*	8	9. viii. 38

* This species, referred to the genus *Amphibdella* by MacCallum (1916), is, according to Chatin's definition in 1874, not a member of this genus. Its exact terminology is being investigated.

Table 3 (*continued*)

Parasite	Host	Locality	Date
DIBOTHRIORHYNCHIDAE Ariola			
Dibothriorhynchus grossum (Rud.)	*Gadus virens*	5	5. viii. 38
" " "	" "	6	8. vii. 39
TETRAPHYLLIDEA			
CEPHALOBOTHRIIDAE Pintner			
Discobothrium fallax van Ben.	*Raja clavata*	3	20. xi. 36
" " "	*Raja montagui*	3	19. i. 37
" " "	*Raja naevus*	6	13. vii. 39
PHYLLOBOTHRIIDAE Braun			
Phyllobothrium lactuca van Ben.	*Hexanchus griseus*	8	9. viii. 38
Phyllobothrium centrurum Southwell	" "	8	"
Anthobothrium auriculatum (Rud.)	*Raja batis*	8	"
Echeneibothrium julievansum Woodland	" "	3	11. xii. 36
" " "	" "	8	9. viii. 38
" " "	*Raja naevus*	6	13. vii. 39
Echeneibothrium variabile van Ben.	*Raja clavata*	3	20. xi. 36
" " "	*Raja montagui*	3	"
" " "	*Raja batis*	3	"
" " "	" "	6	10. vii. 39
Echeneibothrium maculata Woodland	*Raja montagui*	3	19. i. 37
ONCHOBOTHRIIDAE Braun			
Calliobothrium verticillatum van Ben.	*Hexanchus griseus*	8	9. viii. 38
Acanthobothrium coronatum (Rud.)	*Scyliorhinus stellaris*	3	11. xii. 36
" " "	*Scyliorhinus caniculus*	3	15. i. 37
" " "	*Raja batis*	6	10. vii. 39
Onchobothrium uncinatum Rud.	*Raja clavata*	3	11. xii. 36
Scolex pleuronectis Muller	*Limanda limanda*	3	1936–37
" " "	*Conger conger*	6	10. vii. 39
PSEUDOPHYLLIDEA			
AMPHICOTYLIDAE Nybelin			
Eubothrium crassum (block)	*Salmo trutta*	2 (Ystwyth Estuary)	10. v. 38
Parabothrium bulbiferum Nybelin	*Merluccius merluccius*	8	8. viii. 38
Abothrium gadi van Ben.	*Merluccius merluccius*	5	10. viii. 38
PTYCHOBOTHRIIDAE Lühe			
Clestobothrium crassiceps (Rud.)	*Merluccius merluccius*	8	8. viii. 38

In all, eighteen species of Monogenea, three species of Digenea, and twenty species of Cestoda have been recovered from a total of 577 fishes examined. They were distributed as follows: from the deep-sea fishing grounds fourteen species of Monogenea, two species of Digenea and seventeen species of Cestoda, and from the Irish Sea four species of Monogenea, three species of Digenea and nine species of Cestoda. *Amphibdella maccallumi* and *A. flavolineatus* from *Torpedo nobiliana*, and *Dactycotyle merlangi* from *Gadus merlangus* were found only in the Irish Sea. *Calicotyle kroyeri* occurred in both regions, in the Irish Sea in *Raja montagui* and in the deep waters in other species of *Raja*. The remaining Monogenea were found only in the Irish Atlantic Slope and Porcupine Bank, as were the majority of their hosts. Of the cestodes and their hosts *Echeneibothrium maculatum* from *Raja montagui*, *Onchobothrium uncinatum* from *Raja clavata*, and *Eubothrium crassum* from *Salmo trutta* were obtained only from the Irish Sea, six species were common to both areas, namely, *Grillotia erinacea* adult and larva, *Discobothrium fallax*, *Echeneibothrium variabile*, *E. julievansum*, *Acanthobothrium coronatum*, and *Scolex pleuronectis*,

usually in different hosts in the two localities. The remaining eleven species of cestodes were found only in fishes from the deeper waters.

The scarcity of Digenea is probably due to the absence of suitable intermediate hosts especially molluscs. The three species obtained were from *Conger conger* which migrates between deep and shallow water for breeding purposes and doubtless becomes infected in shallow water near the coast. In Monogenea the life cycle is direct, so the problem of intermediate hosts does not arise. In cestodes the intermediate hosts are Crustacea and fishes which would be more widely distributed in the various localities resulting in a more even distribution of the parasites. Host specificity too plays a part. In the Monogenea, owing to their direct development, this is perhaps more easily apparent, as ontogenetic development must depend primarily upon a physiological relation between parasite and host. It is natural therefore to find a group of related parasites exhibiting marked specificity to related hosts, e.g. parasites of the genus *Dactycotyle* are invariably found on fishes of the family Gadidae. This principle, however, cannot be applied generally, there being several exceptions to it. This is illustrated in the family Mazocriidae, the members of which usually occur on the gills of fishes belonging to the family Gadidae, but *Discocotyle leptogaster* of this family occurs on the gills of *Chimaera monstrosa*, a fish not only belonging to a different family but to a different subclass.

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A DESCRIPTION OF THE ANATOMY OF THE MONOGENETIC TREMATODE *CHORICOTYLE CHRYSOPHRYI* VAN BENEDEN & HESSE

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(With 7 Figures in the Text)

Introduction

The specimens of *Choricotyle chrysophryi* van Beneden & Hesse, 1863, used in this study were obtained from the gills of *Pagellus centrodontus* (De la Roche) caught at the Irish Atlantic Slope (lat. 53° 30′–54° N., long. 11° 40′ W., average depth 138 fm.) in August 1938 and July 1939. A total of sixty host specimens was examined, and eleven of these were found to bear the parasite. The maximum degree of infestation encountered was two parasites per host fish.

The genus *Choricotyle* was proposed by van Beneden & Hesse (1863) with *C. chrysophryi* as the type species. Parona & Perugia in 1889 accepted the genus and described a new species *C. Taschenbergii*, but St Remy (1891–2) regarded *Choricotyle* as a subgenus of *Octobothrium* Leuckart, 1827. Cerfontaine (1898), after examining the illustrations of van Beneden & Hesse and of Parona & Perugia of *Choricotyle*, and having considered the relations between parasite affinities and host affinities, was of the opinion that *Choricotyle* might be included in the section Diclidophorinae of the Octocotylidae. St Remy (1898) accepted Cerfontaine's suggestion and transferred *C. chrysophryi* and *C. Taschenbergii* to the genus *Diclidophora* Goto, 1894.

A genus *Diclidophora* had been created by Diesing (1850) to include *D. longicollis* Diesing, 1850 and *D. palmata* Diesing, 1850. The genus was founded in order to separate these species from the genus *Octocotyle* Diesing, 1850 (syn. *Mazocraes* Hermann, 1782, syn. *Octobothrium* Leuckart, 1827, syn. *Octostoma* Kuhn, 1829), the division being based on whether the posterior suckers were pedunculate or sessile. Diesing completely abolished the Trematode genus *Octobothrium* and adopted that name for a Cestode genus with *O. rostellatum* Diesing, 1850 as the type species.

Goto (1894) accepted Diesing's abolition of *Octobothrium*, but emphasized the fact that the real difference between the two replacing genera, namely, *Octocotyle* and *Diclidophora*, was that the former possessed one or two pairs of hooks between the last pair of posterior suckers, whereas the latter did not. Goto accepted Diesing's nomenclature 'because Diesing seemed the first who recognized the difference between the genera in question'. But as Cerfontaine (1896) pointed out, Goto had really created a new genus *Diclidophora*, since

his generic diagnosis to include four new species would not permit the inclusion of the type species of Diesing's *Diclidophora*. In creating the new genus, Goto was apparently unaware that van Beneden & Hesse (1863) had described a very closely allied form under the name of *Choricotyle chrysophryi*. Goto's generic diagnosis allows the inclusion of this species in every respect quoted, and moreover the skeletons of the suckers of Goto's four new species are identical with those of the specimens of *C. chrysophryi* in the writer's possession.

According to the Law of Priority the genus *Diclidophora* Goto, 1894 becomes a synonym of *Choricotyle* van Beneden & Hesse, 1863, and since the name of the type genus is changed, the name of the family must be changed from Diclidophoridae to Choricotylidae.

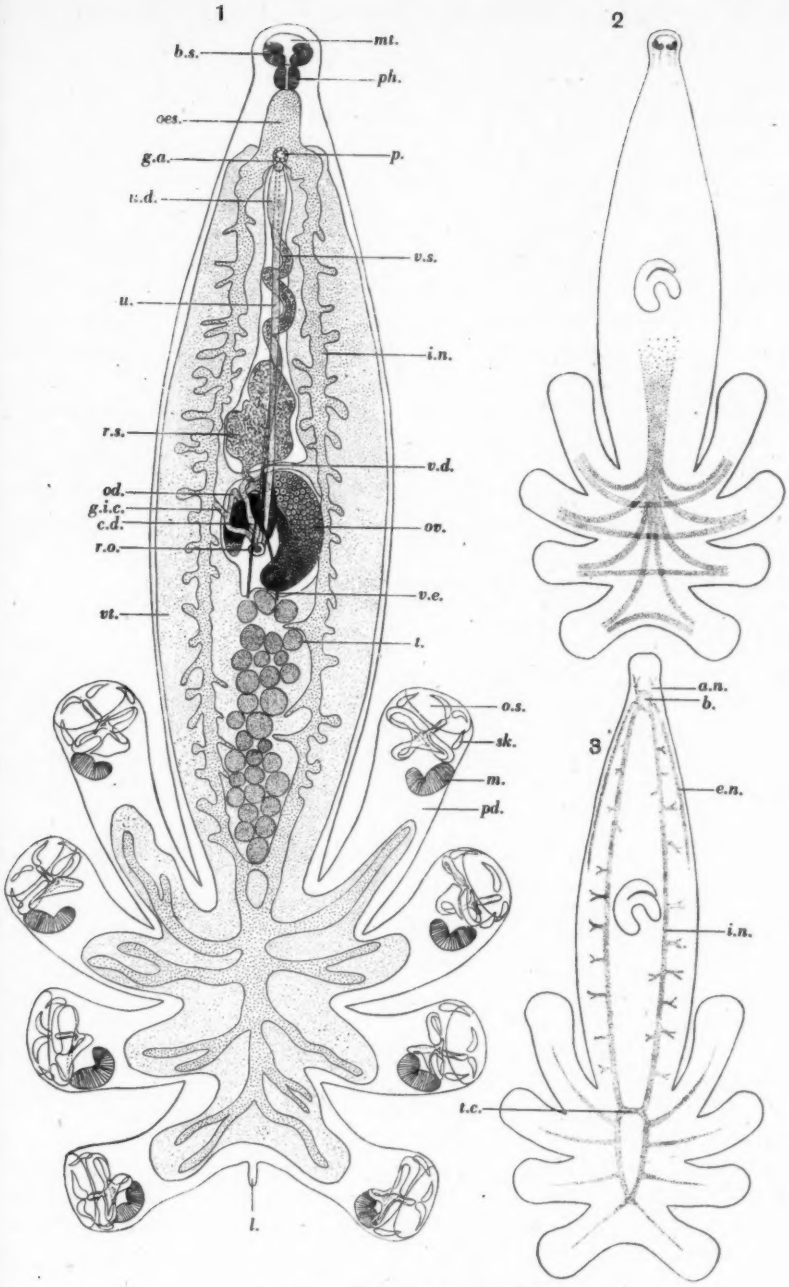
The present record of *Choricotyle chrysophryi* appears to be the first since van Beneden & Hesse founded the species and genus for specimens which they obtained from the gills of *Sparus auratus* (syn. *Chrysophrys auratus*). The original description was incomplete, and the present account, which is more detailed, is based upon a study of serial transverse, longitudinal, and facial sections cut at 6μ and stained with Ehrlich's haematoxylin and eosin.

External morphology, including an account of the structure of the posterior suckers (Figs. 1, 6 and 7)

Fresh specimens of *Choricotyle chrysophryi* are brown, and the animal is of the shape illustrated in Fig. 1. The total length of the parasite is about 5 mm., and the maximum width of the body proper is about 1 mm. The posterior end bears an adhesive organ provided with four pairs of suckers situated at the ends of peduncles. The lengths of these peduncles decrease from before backwards, the most anterior measuring 1·0 mm., and the others 0·75, 0·50 and 0·46 mm. respectively. The anterior peduncles are directed forwards and the posterior ones backwards, the intervening peduncles occupying more or less intermediate positions. This orientation of the peduncles is characteristic of the species.

Situated medianly between the origins of the hindmost pair of peduncles is a very small posteriorly directed appendage 0·11 mm. long and 0·03 mm. wide. A similar structure has been observed in *Choricotyle labracis* by Cerfontaine (1896) and in *Dactycotyle minor* by Gallien (1937), and has been termed 'languette' by these authors. The writer has not been able to trace any references in English to a homologous appendage, and therefore proposes the adoption of the French term 'languette'. It consists of a projection of the body wall containing a core of parenchyma. On account of its small size the languette is not readily discernible in *in toto* preparations. Cerfontaine (1896) observed the languette of *Choricotyle labracis* in section, but could not distinguish it in an *in toto* preparation.

The subterminal mouth is transversely oval, the axes measuring 0·22 and 0·10 mm. Behind the mouth in the median line at a distance of 0·37 mm. on the ventral surface, is the genital atrium. This is a very shallow longitudinally



Figs. 1–3. *Choricotyle chrysophryi.*

Fig. 1. Entire specimen, ventral view. Fig. 2. Main muscular systems.

Fig. 3. Nervous system.

oval depression measuring 0·10 × 0·07 mm. There is no vagina, and the excretory apertures have not been observed.

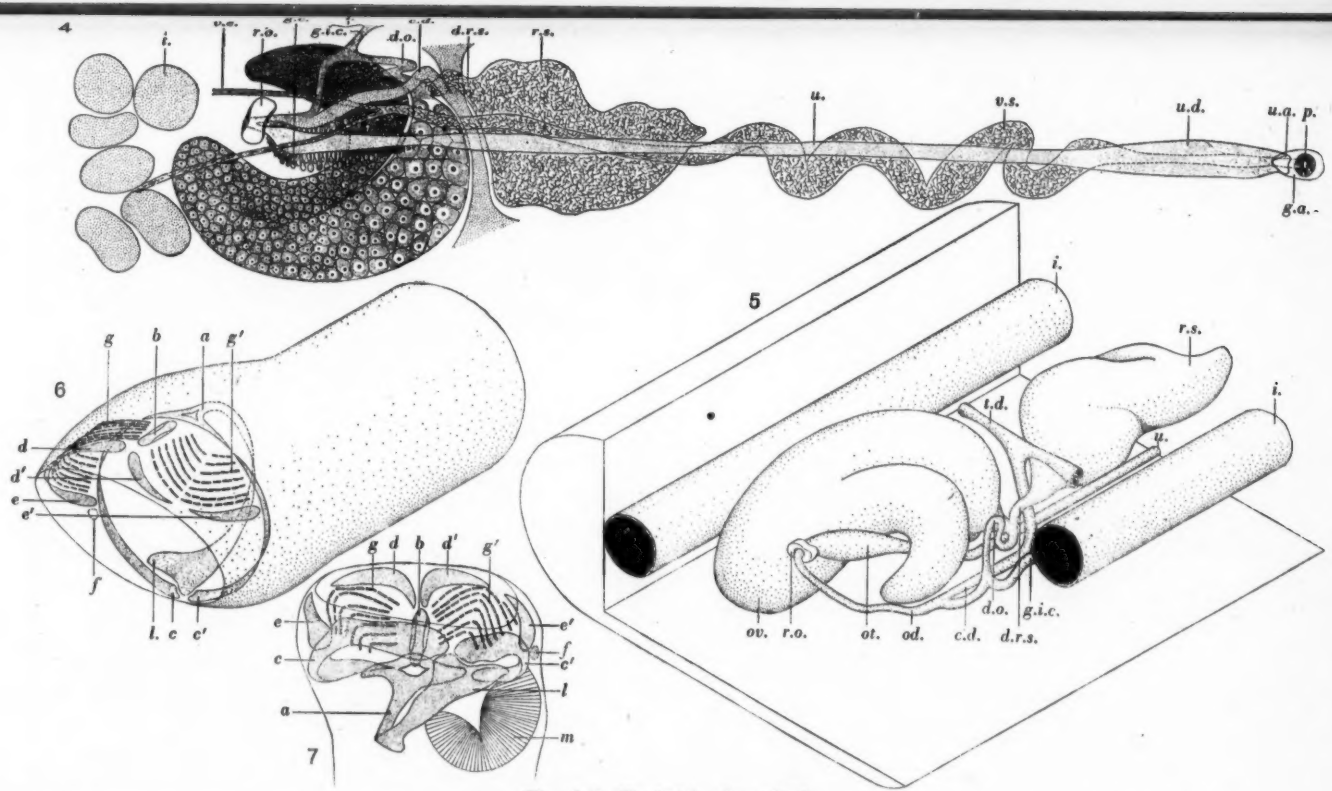
Each sucker of the posterior adhesive organ is cup-like, with a circular or oval aperture, dependent on the degree of contraction of the muscles. However narrowly oval the aperture of the sucker might be, it is not to be confused with the slit-like apertures of the pincer-like adhesive organs characteristic of the Mazocriidae. The aperture of each sucker is not vertical, for owing to an extension of the dorso-lateral walls of the sucker, it becomes directed obliquely ventrally.

In the following description of the arrangement of the skeletal bars, 'anterior' refers to that part of the sucker which would face anteriorly if the peduncle were orientated at right angles to the longitudinal axis of the body, as illustrated by the disposition of the last but one sucker on each side of the animal represented in Fig. 1.

The skeleton of each sucker (Figs. 6, 7) is composed of eight relatively large bars *a*, *b*, *c*, *c′*, *d*, *d′*, *e*, and *e′*, which are consistently present, and a varying number of smaller bars *f*, *g* and *g′*. The two bars *a* and *b* constitute a cruciform arrangement radiating from the dorsal wall of the sucker. Bar *a* is T-shaped, the stem passing from the centre of the cross, first in a proximal direction and then curving through an arc of 180° in a median vertical longitudinal plane to terminate ventrally near the margin of the sucker. The stem of *a* is hollow, but the arms of the T, forming the transverse axis of the cross referred to above, are solid. In its ventral portion bar *a* bears on its posterior border a lamellate extension *l*. The cross is completed by bar *b*, arising near the junction of the arms and stem portions of the T-shaped piece, and passing distally. This bar is hollow, but bears solid lateral aliform extensions. The lateral walls of the sucker are supported by two curved bars *c* and *c′* which arise dorsally near the ends of the arms of the T-shaped piece *a* and pass in opposite directions along a vertical transverse circumference to terminate ventrally near the end of *a*.

Bars *a*, *c*, and *c′* support the hemispherical part of the sucker. The oblique dorsal extension of the wall is supported by the bar *b* already referred to, and by two pairs of solid peripheral bars. The first pair *d* and *d′* arises dorsally near the distal end of *b* and each bar passes obliquely ventrally for about one-eighth of the circumference of the sucker. The second pair *e* and *e′* arises one on each side near the middle regions of *c* and *c′*. Each of the two bars passes dorsally parallel to the margin of the sucker to terminate near the ventral ends of *d* and *d′*.

In addition to the eight bars described above there is present in some suckers of some specimens a very small piece *f* situated laterally near the proximal end of the posterior bar *e*. The presence of piece *f* is apparently an inconstant feature, there being no systematic arrangement of the piece either in particular suckers or in particular specimens. Goto (1894) illustrated a symmetrical pair of such pieces in *Choricotyle smaris*, but Cerfontaine (1896) stated that a piece



Figs. 4–7. ***Choricotyle chrysophryi.***

Fig. 4. Reconstruction of male and female genitalia, excluding majority of testes, in ventral view.

Fig. 5. Hypothetical diagram of ovary and related ducts in postero-dorsal isometric view.

Fig. 6. Hypothetical diagram of posterior sucker of the right side in antero-dorsal isometric view.

Fig. 7. Posterior sucker of the left side, ventral view.

(For explanation of lettering in Figs. 6 and 7 see text.)

corresponding to *f* in *C. chrysophryi* is found only at the posterior borders of the suckers of *C. labracis*.

The dorsal walls of the sucker are further supported by two systems of very small rods *g* and *g'*, arranged superficially inside the muscular walls. Each system consists of about six or seven concentric arcs, each arc containing a varying number of small rods. These systems *g* and *g'* give further support to the regions enclosed by bars *b*, *d*, *e* and part of *c*, and *b*, *d'*, *e'*, and part of *c'* respectively.

The skeletal bars serve both to support the muscular walls of the sucker and as insertions for bundles of fibres continuous with the main muscular systems of the adhesive organ (Fig. 2). In addition there is a well-developed muscular cup (*m* in Figs. 1 and 7) in the depth of the posterior half of each sucker.

Internal anatomy

Alimentary canal (Fig. 1). The mouth leads to a buccal cavity which is provided with a pair of laterally placed hemispherical suckers, each 0·10 mm. in diameter. Behind the buccal cavity is the very muscular pharynx, the external diameter being 0·10 mm., but the lumen averaging only about 0·007 mm. in diameter. The pharynx is succeeded by a wide oesophagus which bifurcates posteriorly to form two main intestinal limbs that lie midway between the dorsal and ventral surfaces of the body. These main intestinal limbs are branched, and unite with each other at their entry into the posterior adhesive organ.

Musculature (Fig. 2). There are two main muscular systems, an anterior in connexion with the buccal suckers, and a posterior in connexion with the adhesive organ.

The buccal suckers are each provided with a pair of muscle bands, one band attached to the inner border of the sucker, and one to the outer. Identical systems have been observed both in *Choricotyle labracis* by Cerfontaine (1896) and in *Cyclobothrium sessilis* (Choricotylidae) by Goto (1894).

The musculature of the posterior adhesive organ is extremely complex, but it is possible to distinguish two very powerful systems lying in the ventral part of the organ. Of these the first consists of a bundle of fibres passing from each peduncle inwards towards the centre and bending anteriorly before meeting its fellow from the opposite side. The union of the eight such bundles forms a powerful median muscle band which has only been traced anteriorly as far as the level of the ovary. A second system consists of four muscular bundles joining the peduncles of one side with the corresponding peduncles of the other, each to each.

Nervous system (Fig. 3). The brain is situated immediately dorsal to the oesophagus, and is a longitudinally ovoid body that gives off three main pairs of nerves, an anterior pair, an external posterior pair, and an internal posterior pair. The anterior nerves arise from the anterior part of the brain and branch to supply the front part of the body. The two posterior pairs of nerves originate

close together in the posterior region of the brain, the external pair arising laterally and the internal pair postero-laterally. The external posterior ventral nerves lie near the lateral margins of the body and become more and more slender as they pass from the brain. It has been found impossible to trace them back beyond the level of the receptaculum seminis. The internal posterior ventral nerves are stouter and continue their courses into the adhesive organ. They lie beneath the main intestinal limbs and give off branches that are approximately coincident in disposition with the diverticula of the alimentary canal. Posteriorly, at the level of the origins of the anterior peduncles, the internal posterior ventral nerves are connected with each other by a well-developed transverse commissure, while at the level of the posterior peduncles they join directly with one another. From this latter junction arises a pair of nerves supplying the fourth pair of peduncles. The other peduncles are also supplied by comparatively stout branches from the internal nerves. The nerves supplying the first pair of peduncles arise posteriorly to the transverse commissure.

Genitalia. (*a*) *Male* (Figs. 1, 4). There are about thirty testes, all situated between the intestinal limbs in the post-ovarian region of the body. Numerous small vasa efferentia unite to form two main ducts that in turn join in the region of the ovary to form a median vas deferens. This passes anteriorly, ventral to the receptaculum seminis and dorsal to the uterus. Beyond the receptaculum seminis it occupies a more dorsal position in the body, and becomes dilated and sinuous in its course, forming a vesicula seminalis. Anteriorly the vesicula seminalis narrows to form a duct that bends ventrally to enter the penis, a spherical muscular organ 0·03 mm. in diameter and armed with a crown of bifid hooks. The penis bears eight hooks in three specimens examined, but in a fourth nine hooks were present.

(*b*) *Female* (Figs. 4, 5). The female genitalia require no special description except in regard to a structure which, as far as the writer has been able to trace, has not been described previously in any Trematode. This structure is a vertically placed ring encircling the oviduct immediately before it enters the ootype. The ring has an external diameter of 0·066 mm. and an internal diameter of 0·018 mm. It consists of a non-nucleated homogeneous matrix, and there are no granular contents to indicate any glandular function. The structure has no direct connexion either with the oviduct or the ootype. It is present in each of three specimens sectioned, and, assuming it to be a constant feature of the species, the writer proposes for it the term 'ring-organ' (*r.o.*).

Although without any apparent direct histological connexion with the female genitalia, the proximity of the 'ring-organ' to these genitalia seems to suggest a possible physiological relation with them. It appears to act as a valve preventing the returning passage of eggs from the ootype to the oviduct, and the mode of functioning would appear to be as follows. The ovum is sufficiently small to pass from the oviduct, through the 'ring-organ' into the ootype. There, if the process in Monogenea is analogous to that in Digenea,

yolk cells and a shell are added to the ovum. The result of the assemblage is an egg much larger than the ovum, and too large to pass through the 'ring-organ'. Then at the contraction of the ootype muscles, the egg can only pass from the ootype in one direction, namely that which leads to the uterus.

In all specimens examined the receptaculum seminis is of relatively enormous size and is distended by the presence of sperms. There is no vagina, and ripe eggs have not been observed.

Discussion

From a consideration of the anatomy, *Choricotyle chrysophryi* seems most nearly related to *C. labracis* (Cerfontaine, 1896) and *C. pagelli* (Gallien, 1937). The chief differences between *C. labracis* and *C. chrysophryi* are that the peduncles are of equal length in the former species and unequal in the latter; that a 'ring-organ' has not been noted in *C. labracis*; and that the receptaculum seminis of *C. labracis*, even when containing sperms, is comparatively much smaller and is spherical in contrast to the more irregular organ of *C. chrysophryi*. *C. pagelli* differs from *C. chrysophryi* in that the origins of its anterior peduncles are contiguous whereas the origins of the anterior peduncles of the latter species are separated by the width of the body; in that there is no languette and apparently no 'ring-organ' in *C. pagelli*; and in further minor details of the female genitalia.

Reference has been made to a terminal languette, a structure which has previously been recorded in *C. labracis* by Cerfontaine. This author suggested that the languette might be functional if it bore hooks, but otherwise it would seem a rudimentary structure. Support for the latter point of view is provided when the size of the languette is considered. It is far too small in comparison with the rest of the worm to be of significance as a hook-bearing appendage. Thus it must be concluded that the languette is a vestigial organ, but whether a vestige of ontogenetic or phylogenetic development remains to be investigated.

In conclusion it must be emphasized that detailed measurements have been given in this description chiefly because other writers upon Trematoda seem to consider them important. In the opinion of the writer, all organs in Monogenea, apart from skeletal structures and hooks, are subject to sufficient variation, according to the degree of contraction or relaxation of the muscles, to render absolute measurements of comparatively little importance. The writer has observed living specimens of numerous species to expand to at least double their contracted length.

Summary

1. *Choricotyle chrysophryi* van Beneden & Hesse has been recorded for the first time since its original discovery in 1863, and from a new host *Pagellus centrodontus* (De la Roche).

2. The history of *C. chrysophryi* and of allied species has been reviewed, resulting in the substitution of the generic name *Choricotyle* van Beneden &

Hesse, 1863 for *Diclidophora* Goto, 1894 and the family name Choricotylidae nov. for Diclidophoridae Fuhrmann, 1928.

3. The anatomy of *Choricotyle chrysophryi* has been investigated by means of serial sections, revealing specialized features in the presence of a terminal languette and of a 'ring-organ'.

ACKNOWLEDGEMENTS. The writer wishes to express his gratitude to Dr F. Gwendolen Rees, under whose supervision this paper was prepared, and to Prof. R. D. Laurie and Dr E. E. Watkin for their interest and encouragement.

Key to Lettering of Figures

a, b, c, c', d, d', e, e', f, g, g',	skeletal bars of sucker	*ot.*	ootype
a.n.	anterior nerve	*ov.*	ovary
b.	brain	*p.*	penis
b.s.	buccal sucker	*pd.*	peduncle
c.d.	common vitelline duct	*ph.*	pharynx
d.o.	dorsal loop of oviduct	*r.o.*	'ring-organ'
d.r.s.	duct of receptaculum seminis	*r.s.*	receptaculum seminis
e.n.	external posterior ventral nerve	*sk.*	skeleton of sucker
g.a.	genital atrium	*t.*	testis
g.c.	gland cells	*t.c.*	transverse commissure connecting internal posterior ventral nerve
g.i.c.	genito-intestinal canal		
i.	intestine	*t.d.*	transverse vitelline duct
i.n.	internal posterior ventral nerve	*u.*	uterus
l.	languette	*u.a.*	uterine aperture
m.	muscle	*u.d.*	dilation of uterus
mf.	mouth	*vt.*	vitellarium
o.s.	oval aperture of sucker	*v.d.*	vas deferens
od.	oviduct	*v.e.*	vas efferens
oes.	oesophagus	*v.s.*	vesicula seminalis

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OBSERVATIONS ON THE GROWTH AND TREMATODE INFECTIONS OF *PERINGIA ULVAE* (PENNANT) 1777 IN A POOL IN THE TAMAR SALTINGS, PLYMOUTH

By MIRIAM ROTHSCHILD

(With 3 Figures in the Text)

Introduction

In several previous publications (Rothschild, 1938, 1939, 1941) attention has been drawn to the variable growth-rate of the brackish water mollusc, *Peringia ulvae*. This intertidal species, which has its maximum abundance between high-water neaps and mid-tide, occurs in great numbers, 32,000 to the square metre, on the mud-flats and saltings of the River Tamar. It was found impossible to arrive at any clear conception of the growth-rate of this snail by collecting samples from the mud-flats, as different curves are obtained for collections made only a few feet apart. It was thought that better results might be arrived at by selecting some well-defined, small, rather isolated and therefore easily recognizable pool in the saltings, from which circumscribed area *P. ulvae* could be collected periodically. In this manner it was hoped to obtain some idea of the growth-rate, at any rate in this particular pool, and also the seasonal fluctuation in the trematode parasites.

Such a pool was duly selected, and although the war has greatly interfered with the number and regularity of the collections, some of the observations made seem worth recording.

A prolonged and fairly detailed study of any animal generally reveals that it is far more variable, both as regards structure and habit, than at first seemed likely. *P. ulvae* is no exception to this, and in fact has proved so capricious that after eight years of intermittent work on this mollusc, there is scarcely any phase or aspect of its life, ranging through growth, breeding, behaviour, development, morphology and parasitism, which I could describe without frequent recourse to such words as usually, typically, probably, apparently. On the whole, however, the population of *P. ulvae* in Pool A (see below) has luckily remained more stable than in the other natural habitats so far studied.

Pool A at Egypt saltings

The pool selected is situated on the periphery of the saltings known as 'Egypt' (see Hartley & Spooner, 1938, pl. xviii). These charming, bird-haunted wastes occupy the zone between high-water springs and high-water ordinary tides. They are raised above the level of the adjacent mud-flats, densely covered with typical salting vegetation and deeply cut into by ramifying

channels. These channels have steep well-scoured sides and soft muddy bottoms, and do not harbour *Peringia*. The mollusc is found well, but not densely, distributed at the roots of the surface vegetation, more especially the grasses. It accumulates in larger numbers in the permanent pools, except those with steep sides, from which it is absent.

Pool A is a shallow permanent pool surrounded by grass, approximately 12 sq. m. in area and some 15–20 cm. deep in the centre. Although the water is definitely shallower round the margin, there is no gradual merging from pool to bank and the edge is well defined. The bottom is covered by a surface deposit of very fine brown mud, a few centimetres deep, below which the mud becomes stiffer and blacker. As the pool is only covered by spring tides it is considerably exposed to the influence of rain and sun, and the salinity fluctuates accordingly. Estimated in November 1940 it proved to be 10·5% or about 30% sea water, and in March 1941 at spring tides 10·1%, but rose to 34% or 97% sea water in July.

Certain points about Pool A favour the study of the growth of the *P. ulvae* found in it. Chief of these is that somewhat mysterious combination of factors which produces rapid increase and maximum size in the species (Rothschild, 1938). Thus the growth curve tends to be spread out and so facilitates the recognition of year groups. The fact that the tides only cover the pool for relatively short periods lessens the chance of a sudden influx of large quantities of weed. At the same time blown leaves do not collect in the bottom—a circumstance seemingly very unfavourable to *Peringia*, and quite frequent in pools high up in the saltings. Finally the small, shallow, yet permanent area of water and the large bird fauna favour a high infection rate with trematode larvae.

The macro-fauna of the pool is fairly dense. *Nereis diversicolor* O. F. Müller occurs in large numbers. *Sphaeroma rugicauda* Leach and *Corophium volutator* (Pallas) are also numerous, although neither can be called dominant species as in certain other pools in the saltings. Small specimens of *Carcinus maenas* L. are also to be taken regularly. No other gastropod apart from *Peringia ulvae* is found, but small specimens of the bivalve *Scrobicularia plana* (Da Costa) are present below the surface mud. A chironomid larva is also abundant. Two oligochaetes occur in vast numbers in the mud, but these, as well as a few minute polychaetes, can scarcely be counted among the macro-fauna, because of their small size. The micro-fauna (including the copepods) was not examined.

A few specimens of *Gobius minutus* Pallas are always present in the pool and occasionally a small elver is taken.

The wading birds undoubtedly visit the pool, as their footprints have been seen in the mud. However, no outer ring of feathers and bird droppings was observed, which is a conspicuous feature of certain areas at St John's Lake, Holbeach, etc., and there is no evidence that a particularly dense congregation of birds gather for roosting or feeding round this particular pool.

Peringia ulvae in Pool A

When the first collection[1] was made in March 1937 attention was drawn to the particular pool by the unusually large size of the infected specimens visible on the surface of the mud. From then onwards to 1941, the population of the pool has been steadily declining. There are certainly not sufficient specimens now to catch the eye. The population of the pool in March 1941, estimated from 8 random sievings, was approximately 100,000 snails (of 1 mm. or over) or one snail per square centimetre.

The snails live principally on or in the layer of brown surface mud, and very few penetrate into the substratum, although dead shells quickly sink into this layer of black mud. So far it has not been possible to determine the factors in

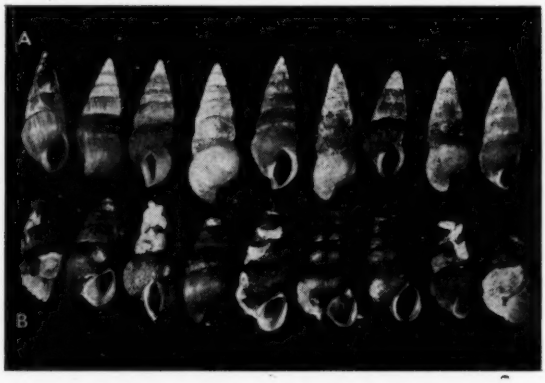

Fig. 1. Living infected specimens of *P. ulvae* (×2). Row A: specimens from saltings of River Camel, Cornwall. Row B: from pool A, Tamar saltings, Devon.

permanent pools which influence the snails to crawl to the surface of the mud at certain times. On the mud-flats the tides seem to play a large part in activating this movement.

In some saltings (Rothschild, 1938) the small specimens seem to collect round the periphery of the pools, but in Pool A the size groups appear more or less evenly distributed, although very large infected specimens tend to keep clear of the edges. There are no weeds in the pool and presumably the snails feed on organic debris in the mud.

The type of *P. ulvae* (Fig. 1, row B) found here has already been described and figured in another publication (Rothschild, 1938). Infected specimens display gigantism and much shell variation. Some may be attenuated, others

[1] About 10,000 specimens were collected on each occasion by scooping mud into a box sieve with a 1 mm. mesh. Subsequently a subsample of the snails was measured and dissected. The November 1939 sample was not dissected, and the smaller specimens of the March 1941 sample were lost through enemy action. Altogether about 100,000 snails were removed from Pool A over a period of two years.

unduly broad and stout, but the most usual type display ballooning of the whorls and gross chipping and corroding of the spire (Fig. 1, row B). This is in marked contrast to the *P. ulvae* infected with the same species of trematode larvae collected from an apparently almost identical habitat in the saltings of the River Camel (Cornwall). In these specimens (Fig. 1, row A) ballooning and chipping of the spires is at an absolute minimum, although their great size is suggestive of infection. It appears therefore that the precise nature of the shell variation produced by the parasites, depends to quite a considerable extent upon the factors governing the type and texture of the shell normally produced by the snail in particular environmental conditions.

Compared with populations of *P. ulvae* from the mud-flats the ratio of uninfected males to females is considerably greater in Pool A. It is therefore possible that the factors which favour increased growth also favour the survival of a larger number of males, or may even influence the development of sex in the immature stages. In this pool, and presumably in the surrounding saltings from which much of the spat must originate, the main spawning period is the autumn. The other regions of the Tamar[1] Estuary such as St John's Lake, it occurs over a more extended period including February and March. The smallest specimens caught by the sieve usually become abundant in February (Fig. 3). At this period specimens of $1\frac{1}{4}$–$1\frac{3}{4}$ mm. constitute the largest group in the sample. By May (Fig. 3) this group has spread out considerably and the peak has shifted to the $2\frac{1}{2}$–$3\frac{1}{4}$ mm. size groups. By July (Fig. 2) no small specimens are taken in the sieve at all. During the months April–July the maximum growth occurs and the autumn spat overtakes the previous year groups and all merge to form a single unit with the peak at about $5\frac{3}{4}$ mm. By November this peak has barely shifted forward $\frac{1}{4}$ mm. A few tiny specimens now begin to be taken in the samples again. These year-old snails, if uninfected, only increase their growth by at most 1 mm. during the rest of their life span, and it is apparent that from March onwards they gradually die off.

This cycle, including the period of maximum and minimum growth confirms the observations made on *P. ulvae* in the laboratory (A. & M. Rothschild, 1939). There does not appear to be any previous accounts of the growth of *P. ulvae* in the wild, and no comparisons are therefore possible.

It will be seen in Figs. 2 and 3 that whereas uninfected snails do not grow beyond $6\frac{3}{4}$ mm. in length, the parasitized specimens attain far greater dimensions. In view of the fact that snails harbouring trematode parthenitae grow faster than uninfected specimens, it seems likely that these giants are no older than the 5–6 mm. groups, but have pushed ahead on account of their parasites. The heaviest mortality of infected snails appears to occur between July and November.

The life cycle of *P. ulvae* in Pool A as outlined above will probably be found to vary somewhat from year to year. This is inevitable in a habitat so much

[1] *P. ulvae* from Hunterston Sands, Millport (Scotland), laid their eggs in May in the laboratory.

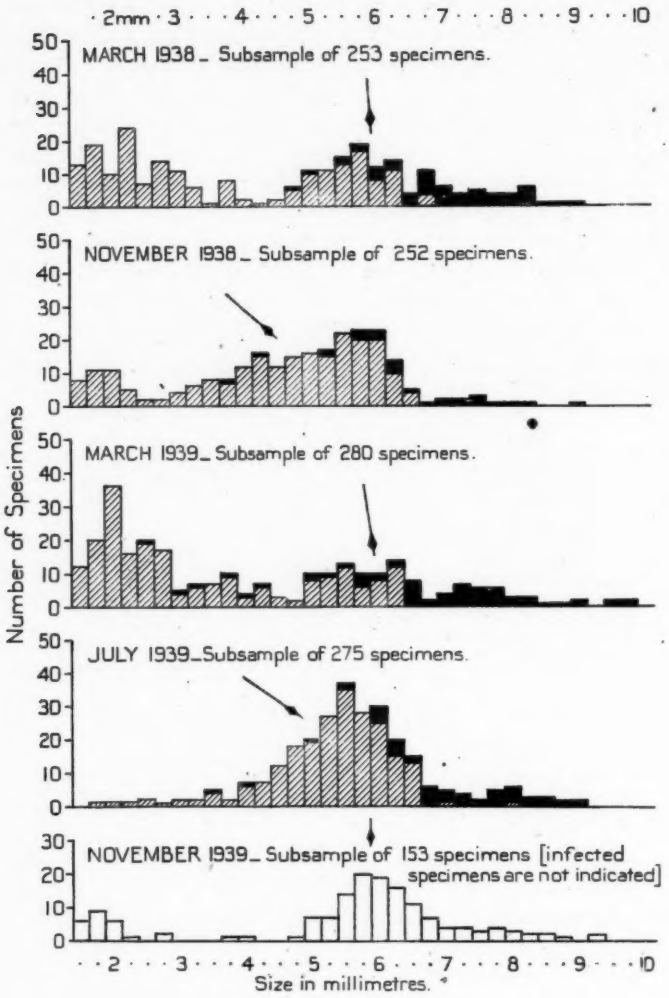
2mm 3 4 5 6 7 8 9 10
MARCH 1938 _ Subsample of 253 specimens.
NOVEMBER 1938 _ Subsample of 252 specimens.
MARCH 1939 _ Subsample of 280 specimens.
JULY 1939 _ Subsample of 275 specimens.
NOVEMBER 1939 _ Subsample of 153 specimens [infected specimens are not indicated]
Number of Specimens
Size in millimetres.

Fig. 2. Subsamples of *P. ulvae* collected from Pool A. The black areas indicate infected specimens, hatched areas uninfected specimens, and the white areas specimens which were measured but not dissected. The connection between year groups in successive periods is indicated by arrows.

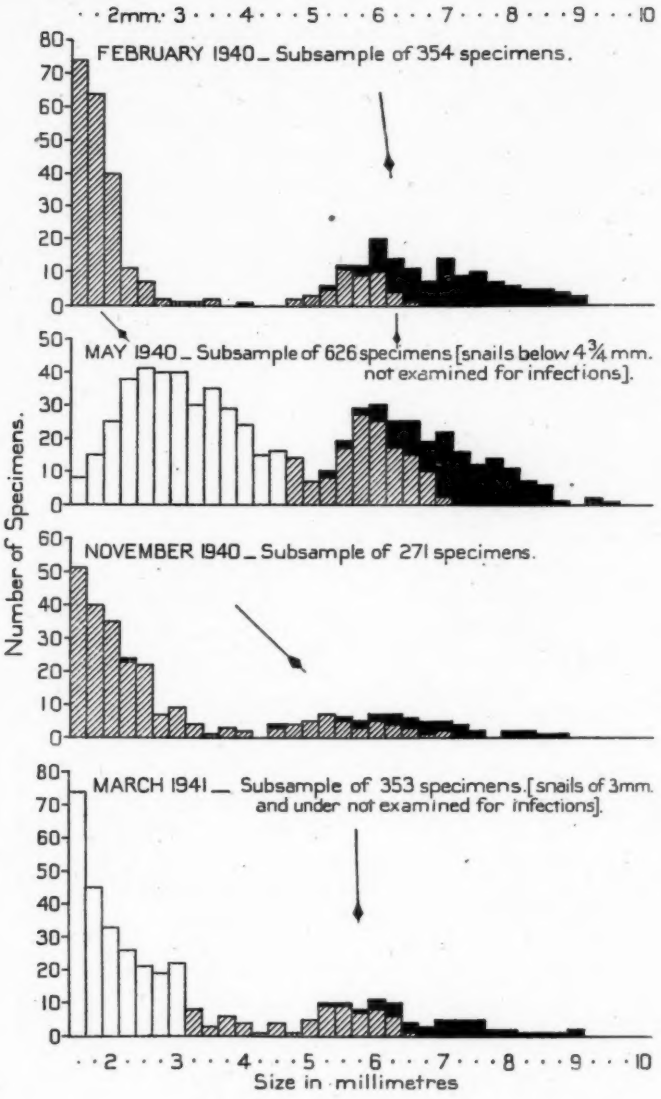
2mm. 3 4 5 6 7 8 9 10
FEBRUARY 1940 _ Subsample of 354 specimens.
MAY 1940 _ Subsample of 626 specimens [snails below 4¾ mm. not examined for infections].
NOVEMBER 1940 _ Subsample of 271 specimens.
MARCH 1941 _ Subsample of 353 specimens. [snails of 3mm. and under not examined for infections].
Number of Specimens.
2 3 4 5 6 7 8 9 10
Size in millimetres

Fig. 3 For explanation, see Fig. 2.

exposed to the influence of the weather.[1] For example, spawning in 1940 was very much earlier than in other years, tiny specimens occurring in large numbers in the November samples. It is almost irresistible to associate this with the unusually prolonged draught of the late summer. At all times, however, except in the midsummer collections, it is possible to distinguish two distinct year groups in the samples obtained. This is in marked contrast to the samples from St John's Lake mud-flats where poorer growth conditions limit the rate of increase and ultimate size of the snails. If samples from this region are measured in $\frac{1}{4}$ mm. groups they generally show only one year group. It will be recalled that spat from both these habitats grew at the same rate and attained the same size when kept under similar conditions in the laboratory (A. & M. Rothschild, 1939).

The trematode fauna of *Peringia ulvae* in Pool A

The rate of infection with parthenitae and cercariae is high, sometimes rising to 28% of the total population above 1 mm. in length. In some samples this means that 70% of the specimens over $3\frac{3}{4}$ mm. are infected. Four main, recognized families of trematodes are represented, the Heterophyidae, Echinostomidae, Microphallidae and Notocotylidae. These constitute 98% of all infections. There are, however, about three other groups found among the remaining 2% of the infections which fit into no known classification. Almost all the species involved have birds as final hosts. The Allocreadiid and Hemiurid cercariae found in *P. ulvae* on the mud-flats are not encountered in Pool A. The only species thought[2] to parasitize a fish as final host is a Heterophyid from the bass. This fish periodically migrates up the river. The cercaria was found once in Pool A during the three years it was under observation.

Conditions in Pool A seem to favour Heterophyids in particular. In the more saline pools in the saltings at the top end of St John's Lake (see Hartley & Spooner, 1938, pl. xviii) far fewer Heterophyids are found, although the bird fauna is essentially similar. The almost total absence of *C. oocysta* in the high saltings (by far the commonest species at St John's Lake) has been noted elsewhere (Rothschild, 1938). It is also to be expected that the Notocotylidae and other duck parasites, although occasionally present in Pool A, are not as common on the upper edge of the saltings as near the main channel where the ducks feed and congregate. More species of this family are found in *P. ulvae* from St John's Lake saltings where they are also numerically about five times as common. The relative numbers of the known families of trematodes found in 100 of the largest snails selected from samples from the two areas in question are compared below (Table 1). Each family is represented by several species.

Taken as a whole the trematode fauna of Pool A, although very rich and varied, displays no unexpected feature. The natural hosts of most of the adult

[1] In December 1939–January 1940 the pool was completely frozen over for several weeks.

[2] Experiments destroyed by enemy action.

worms are not known, but those which are recorded, such as *Cryptocotyle jejuna* Nicoll are from wading birds. There is little doubt that the Charadridae constitute the principal source of infection for *Peringia ulvae* in Pool A.

It is, however, remarkable that true fork-tailed cercariae are conspicuously absent from the saltings. The gulls and other birds become infected at their fresh-water haunts. When they return in winter to the estuaries their droppings are full of eggs of Strigeid worms and probably also the eggs of blood-flukes. This group of parasites readily adapts itself to new first intermediate hosts and it therefore seems likely that the environment presents some factor lethal to the egg or miracidium, thus rendering the highly susceptible *P. ulvae* free from their attack.

The infection rate of *P. ulvae* with cercariae would be expected to reflect the seasonal migration of the estuarine birds, and this to a limited extent is true, but the effect is considerably blurred by the fact that infections can survive for over a year. It is problematical how long infected *P. ulvae* survive in nature, particularly under maximum growth conditions. In the laboratory four years is not at all unusual, but there is reason to suppose that in Pool A eighteen months is about the maximum time.

Table 1

	Hetero-phyidae	Micro-phallidae	Noto-cotylidae	Echinasto-midae	Other groups	Total
Pool, St John's Lake	13	50	16	4	17	100
Pool A, Egypt saltings	63	24	3	7	3	100

The birds return to the estuaries from their summer quarters from August onwards, but when they first arrive are probably not infected with the species attacking *P. ulvae*. This certainly must apply to all the young birds reared the same spring. It has been found that at any rate in the laboratory the heavy trematode infections do not survive many months in the avian host. They tend to decrease greatly in numbers and often disappear altogether. After arrival the birds acquire new infections locally, by consuming the second intermediate host harbouring viable cysts. These infections take a certain time—varying from a few days to several weeks to develop to maturity and produce eggs. The incubation period of the eggs also varies within much the same limits. After the miracidium has penetrated the snail a further period of three to six weeks elapses before free swimming cercariae are produced. It is therefore to be expected that *P. ulvae* will show a relatively low rate of infection in the autumn, although a certain number of infections from the previous spring will be found in the population. The peak of infection will be reached in late winter and early spring after the bird population has reached its height, and has acquired infections locally, and when the subsequent infections of the first intermediate host have had the requisite time in which to develop. It will be seen in Fig. 2 that the maximum infection rate is 33% in March and the minimum 11% November 1939. This high spring infection rate

is reflected in the greater number of 'giant' specimens found in the pool at that period.

Apart from fluctuations in the actual number of infections as a whole, a seasonal variation in the relative abundance of the various families and species might be shown. A more prolonged study of the area is required to establish this with any certainty, as the random movements of large flocks of birds are bound to affect it considerably. It does seem, however, that the relative abundance of Heterophyids and Echinostomes is lowest in the autumn. This may be due to a higher death-rate among the molluscs infected with these species. In the laboratory they exert a more lethal effect than ubiquitous cercariae. Within the family Heterophyidae itself, a somewhat similar example may be found. The Haplorchis group, which certainly seems more lethal than the Cryptocotyle group, represent about 55% of all Heterophyid cercariae in Pool A in March. By November they have fallen to 24%.

General remarks

Perhaps the most satisfactory result of this very incomplete study of *P. ulvae* in Pool A is the confirmation of the experiments carried out in the laboratory. The growth-rate and period of maximum growth displayed by the spat collected from this same pool and reared in captivity under favourable conditions, closely parallels those found in nature.

Under all conditions, however, *P. ulvae* appears to be unusually sensitive to its environment (both external and internal), and its reactions are perhaps more marked than in many other species which respond to similar factors. Few other molluscs show such marked gigantism resulting from parasitism, and although the literature abounds with records of variation in the growth of snails, *P. ulvae* displays this characteristic in an exaggerated form. It is also very interesting to find that the type of shell variation induced by parasitism depends not only on the parasites themselves, but on these in conjunction with external environmental factors. It is quite possible that the degree of gigantism and variation caused in this manner is a fair measure of the lability or instability of the species.

As the first intermediate host of trematodes, both as regards infection-rate and the number of species attacking it, *P. ulvae* is unique among marine and brackish water species. So high is the incidence of parasitism shown in permanent pools, that it would inevitably affect the abundance of the host if the phenomenon was of general occurrence throughout the population found in the estuary. But on the mud-flats, which are teeming with *P. ulvae*, conditions do not favour such a heavy percentage of infection. As these pools high up the saltings are almost certainly restocked, or at any rate added to, by spat brought in at spring tides, parasitism is probably not responsible for the steady decline in the numbers of specimens in Pool A, although it may be a contributory factor.

So varied and numerous are the trematodes found in *P. ulvae* that investigation of their life-histories necessitates the study of all the main groups of animals found in the area, and throws much interesting light on the delicate and intricate ecological balance of the fauna of the saltings and surrounding mud-flats.

SUMMARY

Samples of *Peringia ulvae* were collected and measured on eight occasions, over a period of two years from an isolated pool in the saltings of the River Tamar. Growth conditions in this pool are at a maximum. Spawning occurs in the autumn and the greatest number of small specimens are found in the sieve (1 mm. mesh) in February. Maximum growth takes place during April–July. After ten months of age, uninfected snails which have reached a length of $5\frac{3}{4}$ mm. grow only 1–$1\frac{1}{4}$ mm., and gradually die off from 17 months of age onwards. Infected snails display gigantism and variation and attain dimensions of 9–10 mm. They are probably no older than uninfected specimens measuring $6\frac{3}{4}$ mm. long.

The infection rate is high and shows certain seasonal fluctuations, no doubt linked with the migrations of the wading birds which are the principal final hosts of the trematodes.

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A REVISION OF THE MONOGENEAN FAMILY DICLIDOPHORIDAE FUHRMANN, 1928

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(With 18 Figures in the Text)

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I. Introduction

The substitution of the family name Choricotylidae for Diclidophoridae Fuhrmann, 1928 has been proposed by the writer (1941) in a paper describing the type species of the genotype of the family, namely *Choricotyle chrysophryi* van Beneden and Hesse, 1863. Further investigations of the literature upon all the species previously allocated to the Diclidophoridae have revealed that several taxonomic revisions are necessary. Such revisions have been attempted in this study, which includes summaries of the present state of our knowledge

of each species, and diagrams, which have been adapted from illustrations by other authors, to meet the requirements of a key to the genera and species of the family.

The family name Diclidophoridae was formally proposed for the first time by Fuhrmann (1928), but the group was really founded by Cerfontaine (1896) when he divided the genus *Diclidophora* Goto 1894 into three genera, namely *Diclidophora sensu stricto*, *Cyclobothrium*, and *Heterobothrium*, and re-united these genera into the 'Section des Diclidophorinae' of the Family Octocotylidae.

MacCallum (1917) described four new species of *Diclidophora*, but referred them to the 'Sub-family Octocotylinae van Beneden and Hesse of the Order Trematoda'. This author did not state the name of the family to which the sub-family belonged, and outlined the history of *Diclidophora* without referring to the work of Goto (1894), in which article the genus had been founded.

Dollfus (1922*a*) described a new species under the name of *Cyclobothrium charcoti* and referred it to Cerfontaine's 'Section des Diclidophorinae' of the Octocotylidae. Poche (1926) in his 'Das System der Platodaria' made no reference either to the Diclidophorinae or any of its species, or to the genus *Choricotyle*.

Fuhrmann (1928) promoted Cerfontaine's 'Section des Diclidophorinae' to the rank of a family which he called 'Diclidophoridae Cerfontaine', but since Fuhrmann changed the diagnosis, he really created the new family Diclidophoridae Fuhrmann, 1928. Both Sprehn (1933) and Gallien (1937) repeated Fuhrmann's fallacy of attributing the family name Diclidophoridae to Cerfontaine. It is difficult to comprehend the procedure of Yamaguti (1937 and 1938) in dealing with the systematic position of species belonging to the genera *Diclidophora* and *Cyclobothrium*. In the earlier publication (1937) he referred *Cyclobothrium iniistii* to the Diclidophoridae Cerfontaine, but in the later one (1938), he placed *Diclidophora elongata*, *Cyclobothrium sessilis*, and *C. semicossyphi* in the Octocotylidae van Beneden & Hesse. Yamaguti gave no characters of the respective families in either paper, or any explanation of his procedure.

II. Diagnosis of the Choricotylidae

Class: Trematoda Rudolphi.

Order: Monogenea van Beneden.

Suborder: Polyopisthocotylinea Odhner.

Family: Choricotylidae Llewellyn, 1941.

Polyopisthocotylinea with a posterior adhesive organ bearing suckers having a skeleton of the typical structure shown in the accompanying diagram (Fig. 1).

Genotype. Choricotyle van Beneden & Hesse, 1863.

The above diagnosis is simple yet sufficient to differentiate clearly the four genera of the Choricotylidae from the remainder of the Polyopisthocotylinea. The definition does not differ essentially from that of Cerfontaine (1896) for his 'Section des Diclidophorinae' except that there is no reference to the eight

posterior suckers exhibiting the same degree of development. This allows for the possible inclusion of *Pedocotyle* MacCallum, 1913, previously a member of the Diclidophoridae, if at least some of the suckers of this parasite are found to be of the Choricotylidean type. The diagnosis differs from that of Fuhrmann (1928) in that it specifies the particular type of 'complicated arrangement of the skeleton of the sucker', and in that it makes no reference to any other anatomical features. It thus allows the inclusion of *Diclidophoropsis* Gallien, 1937, which possesses a vagina and which consequently could not be included in Fuhrmann's Diclidophoridae. *Diclidophoropsis* also exhibits a great variation in the structure of the armature of the penis in comparison with that in *Choricotyle*, *Cyclobothrium*, and *Heterobothrium*; thus Fuhrmann's diagnostic feature 'penis with coronet of hooks' is omitted. As for the habitat, the Choricotylidae exhibit a marked tendency to parasitize the gills of marine fishes of the order Percomorphi, and in particular the family Sparidae. But numerous aberrant records, particularly of Choricotylidean super-parasites upon parasitic Copepoda, prevent any reference to habitat being included in the family diagnosis.

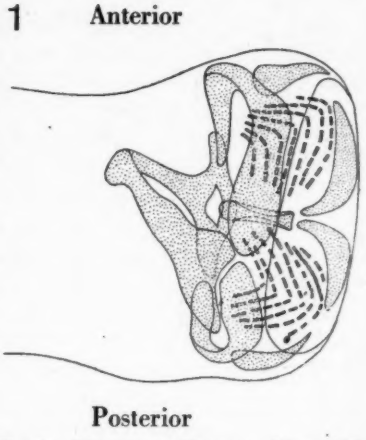

Fig. 1. Diagram to illustrate the typical structure of the skeleton of one of the left posterior suckers of a Choricotylidean, in ventral view.

III. Keys to the genera and species of the family

A. *Key to the genera of the Choricotylidae* (Figs. 2–18)

1. (*a*) Vagina present, penis hooks numerous (more than fifteen) and with single points **Diclidophoropsis**, p. 428
   (*b*) Vagina absent, penis hooks fifteen or less and with double points . . 2
2. (*a*) Testes some anterior and some posterior to the ovary **Cyclobothrium**, p. 426
   (*b*) Testes all posterior to the ovary 3
3. (*a*) Skeletons of anteriormost pair of suckers orientated inversely in comparison with those of three posterior pairs **Heterobothrium**, p. 427
   (*b*) Skeletons of all suckers occupy same relative orientation **Choricotyle**, p. 419

B. *Key to species of the genus* Choricotyle

1. (*a*) Body proper (i.e. not including posterior adhesive organ) clearly divisible into two regions 2
   (*b*) Body proper not divisible into two regions 4

2. (*a*) Anterior part of body proper demarcated from posterior by distinct shoulders **C. charcoti**, p. 424
   (*b*) Two regions of the body merge imperceptibly into one another **3**

3. (*a*) Anterior part of body attenuated to form long narrow neck, posterior part broad **C. smaris**, p. 420
   (*b*) Anterior part of body spatulate and expanded, posterior part slender **C. affine**, p. 422

4. (*a*) Peduncles of unequal lengths **5**
   (*b*) Peduncles all of equal length **8**

5. (*a*) Posterior peduncles developed more than anterior **C. merlangi**, p. 422
   (*b*) Anterior peduncles developed more than posterior **6**

6. (*a*) Three anterior pairs of peduncles of equal size and relatively large, posterior pair relatively small **C. neomaenis**, p. 423
   (*b*) Peduncles progressively shorter in antero-posterior succession . . . **7**

7. (*a*) Origins of anteriormost pair of peduncles separated by the width of the body **C. chrysophryi**, p. 419
   (*b*) Origins of anteriormost peduncles contiguous **C. pagelli**, p. 424

8. (*a*) Mouth terminal and comparatively large **C. cynoscioni** p. 423
   (*b*) Mouth sub-terminal and comparatively small **9**

9. (*a*) Penis with thirteen double-pointed hooks **C. prionoti**, p. 423
   (*b*) Penis with eight double-pointed hooks **10**

10. (*a*) Body proper oval, anterior end obtuse. Peduncles comparatively short and robust **C. labracis**, p. 422
    (*b*) Body proper lanceolate, anterior end rather narrow. Peduncles comparatively long and slender **C. elongata**, p. 420

C. *Key to species of the genus* Cyclobothrium

1. (*a*) Pre-ovarian testes occupying whole of the intercaecal field **C. sessilis**, p. 426
   (*b*) Pre-ovarian testes arranged in two submedian rows **2**

2. (*a*) Total number of pre-ovarian testes 3–6 **C. iniistii**, p. 426
   (*b*) Total number of pre-ovarian testes 10–20 **C. semicossyphi**, p. 426

IV. SYSTEMATIC REVIEW OF THE GENERA AND SPECIES OF THE CHORICOTYLIDAE

Genus. Choricotyle van Beneden & Hesse, 1863 (Figs. 2–12).

Diagnosis. Choricotylidae with penis armed with coronet of double-pointed hooks numbering fifteen or less. Testes all posterior to ovary. Skeletons of posterior suckers all orientated in the same direction relative to the longitudinal axis of the body. Vagina absent.

The history of the genus has been reviewed in a previous paper by the writer (1941).

Species of Choricotyle

(1) *Choricotyle chrysophryi* van Beneden & Hesse, 1863 (Fig. 5).

Diagnosis. Body proper not divisible into two regions; peduncles progressively shorter in antero-posterior succession, with origins of foremost pair

separated by the width of the body. With terminal languette. Number of penis hooks = 8 or 9. This species has been the subject of an investigation by the writer (1941). The excretory system and details of the musculature remain to be described.

(2) *Choricotyle smaris* (Goto, 1894) (Fig. 12).

Syn. *Octobothrium smaris* Ijima (in MS. referred to by Goto, 1894).
Syn. *Diclidophora smaris* Goto (1894).

Diagnosis. Body proper divisible into two regions which merge imperceptibly into one another, a posterior part broad and an anterior part attenuated to form a long neck. Number of penis hooks = 6.

C. smaris was originally found by Max V. Brunn on a *Cymothoa* in the buccal cavity of *Smaris vulgaris*. A single specimen of the parasite was forwarded to Prof. Ijima at the College of Science of the Imperial University of Japan, who, in a manuscript that was not published (Goto, 1894), named the species *Octobothrium smaris*. Deickhoff in 1891 assumed *O. smaris* to be a synonym of *O. merlangi*, but Goto (1894) made a thorough investigation of *O. smaris* and demonstrated that the two species were distinctly separate. Goto described the species as '*Diclidophora smaris* (Ijima MS.)', but Cerfontaine (1896) attributed the specific name to Goto. Since Ijima's manuscript does not appear to have been published, Cerfontaine's procedure is correct according to the International Code, and the name of the parasite is now *Choricotyle smaris* (Goto). The species does not appear to have been recorded since the work of Goto (1894).

(3) *Choricotyle elongata* (Goto, 1894) (Fig. 11).

Syn. *Diclidophora elongata* Goto, 1894.

Diagnosis. Body proper not divisible into two regions but lanceolate with the anterior end narrowly attenuated; peduncles all of equal length and comparatively long and slender; mouth subterminal; number of penis hooks = 8.

Choricotyle elongata was obtained by Goto (1894) from the mouth cavity of *Pagrus tumifrons*, and occasionally on specimens of *Cymothoa* parasitizing

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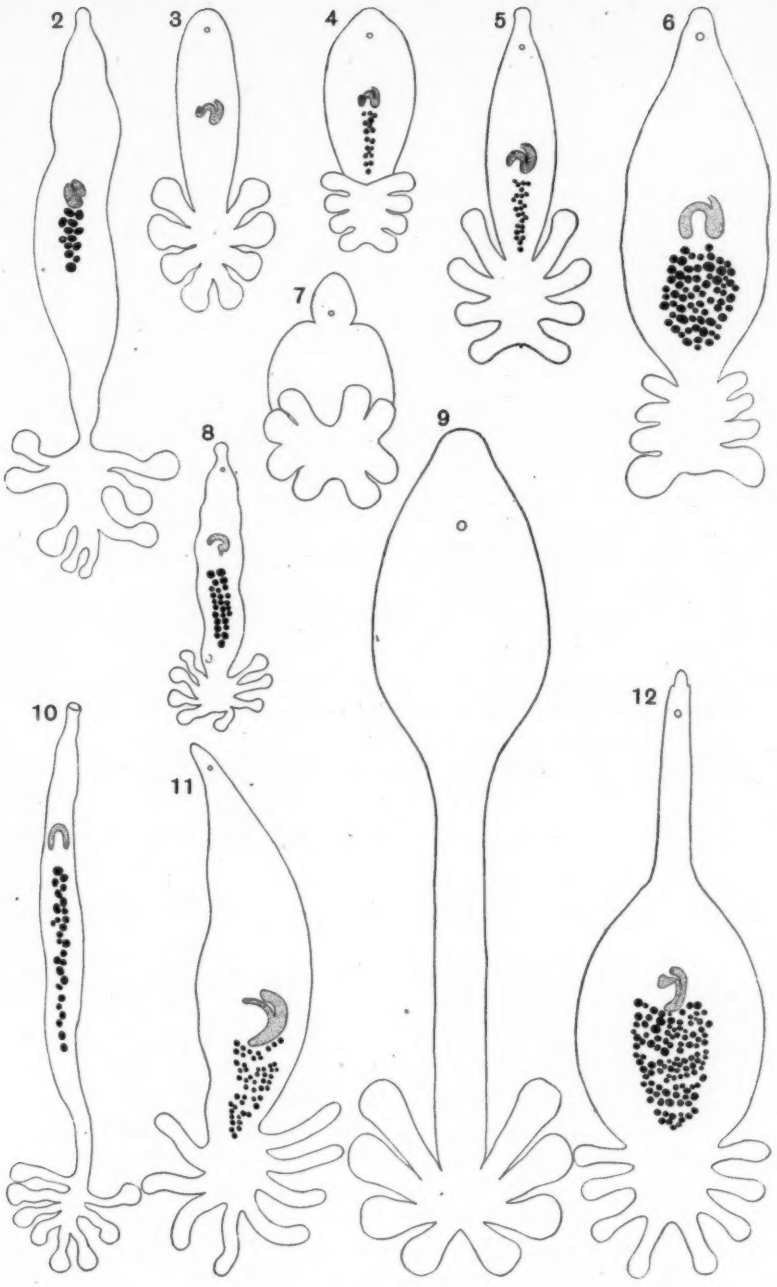
Legends to Figs. 2–12

Figs. 2–12. Species of *Choricotyle*, diagrams adapted after the various authors indicated below, and all drawn to the same magnification (× 10).

Fig. 2. *C. neomaenis*. Adapted after MacCallum (1917).
Fig. 3. *C. labracis*. Adapted after Cerfontaine (1896).
Fig. 4. *C. pagelli*. Adapted after Gallien (1937).
Fig. 5. *C. chrysophryi*. Original.
Fig. 6. *C. merlangi*. Adapted after MacCallum (1917).
Fig. 7. *C. charcoti*. Adapted after Fuhrmann (1928).
Fig. 8. *C. prionoti*. Adapted after MacCallum (1917).
Fig. 9. *C. affine*. Adapted after Linton (1898).
Fig. 10. *C. cynoscioni*. Adapted after MacCallum (1917).
Fig. 11. *C. elongata*. Adapted after Goto (1894).
Fig. 12. *C. smaris*. Adapted after Goto (1894).



Figs. 2–12.

the mouth cavity of this fish. Goto made a thorough investigation of *Choricotyle elongata*, and his description has been added to by Yamaguti (1938). This latter work was made possible by the discovery of four specimens of *C. elongata* as super-parasites of *Meinertia oestroides* parasitic in the mouth-cavity of *Pagrosomus unicolor*. Apart from those of Goto and Yamaguti, there appear to be no other records of *Choricotyle elongata*.

(4) *Choricotyle labracis* (Cerfontaine, 1896) (Fig. 3).

Syn. *Diclidophora labracis* Cerfontaine, 1896.

Diagnosis. Body proper not divisible into two regions, but oval with the anterior end broadly rounded; peduncles all of equal length, comparatively short and robust; with a terminal languette; number of penis hooks = 8.

Choricotyle labracis was first recorded by Cerfontaine (1896) from the gills of *Morone labrax* (L.) syn. *Labrax lupus* Day, and was the subject of a detailed investigation by this author. The parasite does not seem to have been otherwise recorded.

(5) *Choricotyle affine* (Linton, 1898) (Fig. 9).

Syn. *Octoplectanum affine* Linton, 1898.
Syn. *Diclidophora affinis* Linton, 1901 [according to Gallien (1937)].

Diagnosis. Body proper divisible into two regions which merge imperceptibly into one another, the anterior part being spatulate and expanded and the posterior part slender; number of penis hooks = 15; eggs fusiform with very long attenuated poles.

The only record of *Choricotyle affine* appears to be that from the mouth of *Paralichthys dentatus* by Linton (1898). The description that accompanied this record was not well done.

(6) *Choricotyle merlangi* (MacCallum, 1917) (Fig. 6).

Syn. '*Diclidophora merlangi* Kuhn, 1829', MacCallum, 1917.

Diagnosis. Body proper not divisible into two regions; peduncles diminishing in size in postero-anterior succession; number of penis hooks = 13–15; egg long and narrow with short filament at posterior pole.

Choricotyle merlangi was first described under the name of *Diclidophora merlangi* Kuhn by MacCallum (1917). This author obtained eight specimens of the parasite from twelve specimens of a host species which he confused under the names of *Urophycis chuss* and *Merluccius bilinearis*. While admitting that the necessary reference by Kuhn (1829) was not available for his consultation, MacCallum decided to call the parasite by the name of *Diclidophora merlangi* Kuhn 'in order to avoid multiplying species'. As pointed out by Dollfus (1922*a*), the worm commonly referred to under the specific name '*merlangi* Kuhn' belongs to the genus *Dactycotyle* van Beneden and Hesse, and was never described by Kuhn. Over a score of noted workers upon Monogenea have

repeated a false reference in relation to '*merlangi* Kuhn', namely, '*Memoires du Muséum d'histoire naturelle*, t. XVIII, 1829 (or 1830)'. In this article Kuhn described *Octostoma alosae* and *O. scombri*, the descriptions being as inaccurate as to refer to the mouth as an anus and to the pedunculate suckers as being anterior. According to Dollfus the name '*merlangi*' in relation to the species now known as *Dactycotyle merlangi* must be attributed to Nordmann, who described the species in 1832. Thus, were the name '*merlangi* Kuhn' still valid a new name for the *Diclidophora merlangi* of MacCallum would be necessary; but since, as described above, there has never been an animal bearing a legitimate name '*merlangi* Kuhn' the name *merlangi* is quite in order for a species of *Choricotyle*, but has to be attributed to a new author, namely, MacCallum (1917). The net result of the above complicated histories is that the name '*merlangi*' remains valid for two species, one *Choricotyle merlangi* MacCallum, 1917 and the other *Dactycotyle merlangi* (Nordmann, 1832).

The anatomy of *Choricotyle merlangi* has been fairly well described by MacCallum, who, however, made no reference to a genito-intestinal canal. Thus, since all other members of the Polyopisthocotylinea appear to possess a genito-intestinal canal, a re-description of *C. merlangi* is necessary.

(7) *Choricotyle prionoti* (MacCallum, 1917) (Fig. 8).

Syn. *Diclidophora prionoti* MacCallum, 1917.

Diagnosis. Body proper not divisible into two regions; peduncles all of the same length; mouth subterminal and comparatively small; number of penis hooks = 13.

The only published description of the species appears to be the original one, namely, that of MacCallum (1917), who obtained his material from *Prionotus carolinus*. This description was of the same standard as that of *Choricotyle merlangi* referred to above, and made the same omission in regard to a genito-intestinal canal.

(8) *Choricotyle cynoscioni* (MacCallum, 1917) (Fig. 10).

Syn. *Diclidophora cynoscioni* MacCallum, 1917.

Diagnosis. Body proper not divisible into two regions; peduncles all of the same length; mouth terminal and comparatively large; number of penis hooks not known.

The original and only record of the species was by MacCallum (1917) from the gills of *Cynoscion regalis*. A re-description of the parasite is necessary since the penis hooks of MacCallum's specimen could not be counted, no eggs were observed, and there was no mention of a genito-intestinal canal.

(9) *Choricotyle neomaenis* (MacCallum, 1917) (Fig. 2).

Syn. *Diclidophora neomaenis* MacCallum, 1917.

Diagnosis. Body proper not divisible into two regions; three anterior pairs of peduncles of equal size and relatively large, posterior pair relatively small; number of penis hooks = 12.

The only record of this species appears to be that from the gills of *Neomaenis analis* reported by MacCallum (1917). A further investigation of the animal is necessary in order to determine the character of the eggs and to ascertain the presence or absence of a genito-intestinal canal.

(10) *Choricotyle charcoti* (Dollfus, 1922*a*, *b*) (Fig. 7).

Syn. *Cyclobothrium charcoti* Dollfus, 1922.
Syn. *Diclidophora 'species'* Fuhrmann, 1928.

Diagnosis. Body proper clearly divisible into two regions, the anterior part being demarcated from the posterior by a pair of distinct shoulders; number of penis hooks = 6; eggs fusiform with very short polar filaments.

The species *Choricotyle charcoti* was founded by Dollfus (1922*a*) who recorded the worm as a superparasite of *Cymothoa* (*Meinertia*) *oestroides* itself parasitic in the buccal cavity of *Trachurus trachurus*. Dollfus referred the animal to the genus *Cyclobothrium* solely on the character of the peduncles which were short, 'almost sessile'. In a later publication Dollfus (1922*b*) figured a specimen of *C. charcoti* in which the suckers were definitely pedunculate, thus the only reason for including the specimen in the genus *Cyclobothrium* was no longer valid.

Dollfus, in his identification, apparently paid no attention to Cerfontaine's diagnoses in regard to internal anatomy, for he remarked that the internal organization of all the species of the Diclidophoridae was the same. Thus Dollfus did not record the disposition of the testes.

According to the diagnoses proposed in this paper, the generic affinity of *C. charcoti* would be indeterminate until further information is obtained as to the position of the testes. However, Fuhrmann (1928) has drawn but not described a parasite under the name of *Diclidophora 'species'* and which, in the opinion of the writer, is identical with Dollfus's *Cyclobothrium charcoti*. Fuhrmann obtained his material from an unspecified marine Isopod. He gave no reasons for his identification of the parasite, but included the work of Cerfontaine (1896) in his references, and omitted that of Dollfus. Then, supposing the identification to be according to Cerfontaine's generic diagnoses, it can be assumed that all the testes are situated posterior to the ovary. Thus both *Cyclobothrium charcoti* Dollfus and *Diclidophora 'species'* Fuhrmann become synonyms of *Choricotyle charcoti* (Dollfus, 1922*a*, *b*).

The internal anatomy of *Choricotyle charcoti* has not been described.

(11) *Choricotyle pagelli* (Gallien, 1937) (Fig. 4).

Syn. *Diclidophora pagelli* Gallien, 1937.

Diagnosis. Body proper not divisible into two regions; peduncles progressively shorter in antero-posterior succession, with the origins of the anteriormost pair of peduncles contiguous; number of penis hooks = 8.

The only specimen of *Choricotyle pagelli* ever recorded was discovered on the gills of *Pagellus centrodontus* by Gallien (1937), who made a detailed investi-

gation of the anatomy of the parasite. The results of this investigation showed that the morphology of *Choricotyle pagelli* bears a striking resemblance to that of *C. chrysophryi*, the greatest difference being that in the former the origins of the anteriormost pair of peduncles are contiguous, whereas in the latter they are separated from each other by the width of the body. In addition there is a great similarity in the habitats so far recorded for these parasites. Both have been recorded from the gills of the same host, *Pagellus centrodontus*, captured in a similar locality, namely the Irish Atlantic Slope Fishing Grounds. Thus the synonymy of *Choricotyle pagelli* with *C. chrysophryi* must be considered.

(12) *Choricotyle* (?) *Taschenbergii* Parona & Perugia, 1889.

This must be regarded as a very doubtful member of the genus *Choricotyle*. Several authors have referred to the species without giving descriptions, and the writer has been unable to obtain the publication in which the original description is reported to be, namely:

Parona & Perugia (1889). *Annali Museo civico Genova*, **27**, (2) VII, 1 Oct. 740–7.

Cerfontaine (1896), referring to *C. Taschenbergii*, stated that from examination of the figure given by Parona & Perugia, the worm would appear to possess two vaginae opening in the neighbourhood of the genital atrium. If this be so, then *C. Taschenbergii* cannot be included in the genus *Choricotyle*, but might possibly be included in *Diclidophoropsis*.

Genus. Cyclobothrium Cerfontaine, 1896 (Figs. 15–17).

Diagnosis. Choricotylidae with penis armed with coronet of double-pointed hooks, which, for all species yet described, are six in number. Testes, some posterior and some anterior to the ovary. Skeletons of posterior suckers all orientated in the same direction relative to the longitudinal axis of the body. Vagina absent.

The genus *Cyclobothrium* was founded by Cerfontaine (1896) in order to accommodate *C. sessilis* (Goto, 1894). This species had previously been referred to the genus *Diclidophora* Goto, 1894, but Cerfontaine applied a stricter interpretation of Goto's diagnosis, and this necessitated the removal of *D. sessilis* to a new genus which he called *Cyclobothrium*. In the opinion of the writer Cerfontaine's revision of *Diclidophora* and his foundation of the genera *Cyclobothrium* and *Heterobothrium* were justified, but his diagnoses of the new genera were too restricted, the result of being based on studies of single species of the genera in question. Since the publication of Cerfontaine's work, Yamaguti (1937, 1938) has described two new species of *Cyclobothrium*, namely *C. iniistii* and *C. semicossyphi*. After examining these descriptions by Yamaguti, the writer suggests the omission of such of Cerfontaine's generic characters as 'lobed receptaculum seminis', and the substitution of the diagnosis proposed in this paper.

Species of Cyclobothrium

(1) *Cyclobothrium sessilis* (Goto, 1894) (Fig. 15).

Syn. *Diclidophora sessilis* Goto, 1894.

Diagnosis. 'Testes exceedingly numerous, extending from a little behind the common genital opening to the level of the first pair of posterior suckers, and occupying the whole region enclosed by the two intestinal trunks' (Goto, 1894). 'Number of penis hooks = 6. Ellipsoidal egg 165–171μ × 75–81μ, and provided at one end with a long coiled filament' (Yamaguti, 1938).

Cyclobothrium sessilis has been recorded from the buccal cavity of *Chaerops japonicus* by Goto (1894) and from the gills of *Semicossyphus reticulatus* by Yamaguti (1938). The species was described in detail by Goto, and minor additions to this account were made by Yamaguti.

(2) *Cyclobothrium iniistii* Yamaguti, 1937 (Fig. 16).

Diagnosis. 'The rounded testes are divided by the ovarian complex into two groups; the anterior testes, only 3 to 6 in all, lie in the two submedian rows in front of the ovary, while the posterior testes, 17 to 23 in number, are massed together in one layer or two behind the ovary. Number of penis hooks = 6. Egg—large, elliptical, 144μ long and provided at one end with an exceedingly long closely coiled filament' (Yamaguti, 1937). Yamaguti's record of the species from the gills of *Iniistius dea* appears to be the only occasion on which the parasite has been collected. This record was accompanied by a short description and a clear diagram of the worm.

(3) *Cyclobothrium semicossyphi* Yamaguti, 1938 (Fig. 17).

Diagnosis. 'Anterior testes 10–20 in number, in two sub-median rows; posterior testes 20–40 in number. Number of penis hooks = 6. Egg—150–160μ long with long coiled polar filament' (Yamaguti, 1938).

Yamaguti obtained his specimens of *Cyclobothrium semicossyphi* from the gills of *Semicossyphus reticulatus*, and this appears to be the only record of the species. Yamaguti has given a good account of the anatomy of the parasite, and included a clear diagram in his work.

Genus. Heterobothrium Cerfontaine, 1896 (Fig. 13).

Diagnosis. Choricotylidae with penis armed with a coronet of double-pointed hooks, which, in the only species as yet referred to the genus, are ten in number. Testes all posterior to the ovary. Skeletons of anteriormost pair of the posterior suckers orientated inversely in comparison with those of the other three posterior pairs. Vagina absent.

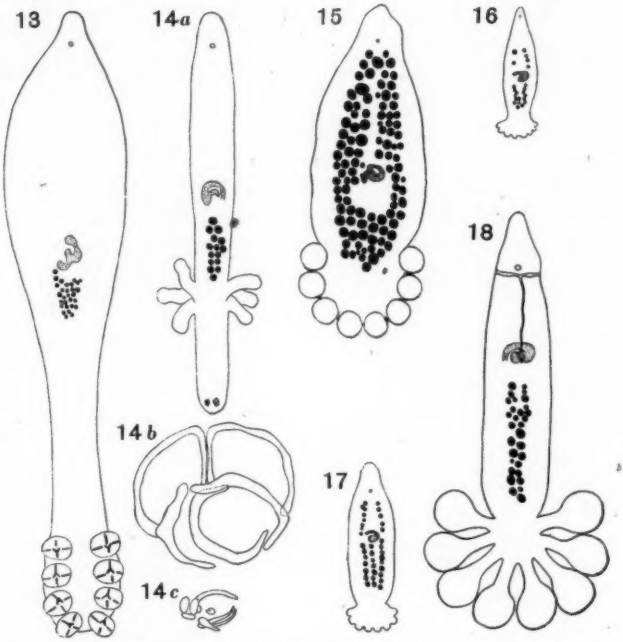
The genus *Heterobothrium* was proposed by Cerfontaine (1896) with *H. tetrodonis* (Goto, 1894) as the type species. The parasite had previously been included in the genus *Diclidophora* Goto, but on Cerfontaine's imposition of a stricter diagnosis for this genus, it became necessary to found a new genus *Heterobothrium* for *H. tetrodonis*. No other species has been included in the genus.

Species of Heterobothrium

(1) *Heterobothrium tetrodonis* (Goto, 1894) (Fig. 13).

Syn. *Diclidophora tetrodonis* Goto, 1894.

Diagnosis. Since this is the only species as yet referred to the genus, no really significant specific characters can be formulated. The species was recorded by Goto (1894) from the gills of *Tetrodon 'sp.'*, and was well described by that author.



Figs. 13–18. Species of the genera *Cyclobothrium*, *Heterobothrium*, and *Diclidophoropsis*, of the Choricotylidae, and of the genus *Pedocotyle* MacCallum, 1913 of uncertain affinity. All figures after the various authors indicated below, and drawn to the same magnification.

Fig. 13. *Heterobothrium tetrodonis*. Adapted after Goto (1894).
Fig. 14*a*. *Pedocotyle morone*. Adapted after MacCallum (1913*a*).
Fig. 14*b*. *Pedocotyle morone*. After MacCallum (1913*a*).
Fig. 14*c*. *Pedocotyle morone*. After MacCallum (1913*a*).
Fig. 15. *Cyclobothrium sessilis*. Adapted after Goto (1894).
Fig. 16. *Cyclobothrium iniistii*. Adapted after Yamaguti (1937).
Fig. 17. *Cyclobothrium semicossyphi*. Adapted after Yamaguti (1938).
Fig. 18. *Diclidophoropsis tissieri*. Adapted after Gallien (1937).

Genus. Diclidophoropsis Gallien, 1937 (Fig. 18).

Diagnosis. Choricotylidae with penis armed with numerous single-pointed hooks, which, in the only species as yet reported to the genus, number 128. Testes all posterior to the ovary. Skeletons of posterior suckers all orientated

in the same direction relative to the longitudinal axis of the body. Two vaginae present.

The genus *Diclidophoropsis* was founded by Gallien (1937) with type species *D. tissieri*. No other species has been reported to the genus.

Species of Diclidophoropsis

(1) *Diclidophoropsis tissieri* Gallien, 1937 (Fig. 18).

Diagnosis. As no other species have yet been referred to the genus, it is impossible to differentiate specific characters from those included in the generic diagnosis given above.

Gallien (1937) recorded the species from the skin of *Macrurus laevis*, and gave a good description of the parasite.

Genus of uncertain affinity: Pedocotyle *MacCallum*, 1913 (Figs. 14 *a*, *b*, *c*)

Diagnosis (with quotations from MacCallum (1913*a*)): Polyopisthocotylinea with penis armed 'not very plentifully with good sized hooklets'. Testes all posterior to the ovary. Six pedunculate suckers 'strengthened by a peculiar chitinous formation as shown in figures' (Fig. 14 *b*). 'At or near the caudal extremity are two more suckers but these are smaller and of a different chitinous structure, as shown in the figure' (Fig. 14 *c*). 'The covering membrane of all the suckers seems also to be reinforced either by chitinous filaments or muscular striae regularly arranged across the space between the larger chitinous structures.... It is impossible to see the vaginal opening.'

The genus *Pedocotyle* was founded by MacCallum (1913*b*) to replace *Podocotyle* MacCallum (1913*a*), a name which MacCallum had discovered to be preoccupied by *Podocotyle* Dujardin, 1845 (Digenea: Allocreadiidae).

Fuhrmann (1928) modified his diagnosis of the Diclidophoridae so that the family might include *Pedocotyle*, but the diagnosis of the Choricotylidae proposed in this paper will not permit the inclusion of the genus, which therefore, for the present, must remain a 'genus of uncertain affinity'.

Species of Pedocotyle

(1) *Pedocotyle morone* MacCallum, 1913 (Figs. 14 *a*, *b*, *c*).

Diagnosis. Since no other species has been added to the genus, it is impossible to separate characters of specific significance from those now credited with generic significance.

P. morone was recorded as a parasite of the gills of *Morone americana* by MacCallum (1913*a*) who also described the species. According to the diagram given by MacCallum this trematode does not possess a genito-intestinal canal. The same author has described at least four other Monogenea, namely *Choricotyle merlangi*, *C. prionoti*, *C. cynoscioni*, and *C. neomaenis*, with no mention of the presence or absence of a genito-intestinal canal, whereas its presence in Polyopisthocotylineans is one of the few constant features of the

sub-order. Then, on account of both this feature and of the poor quality of the description of the skeletons of the suckers, a re-description of *Pedocotyle morone* is necessary.

V. AFFINITIES OF THE CHORICOTYLIDAE

The members of the Polyopisthocotylinea with which the Choricotylidae appear to have most in common are some of the Mazocriidae. In particular there is a striking resemblance between both the external morphology and the internal anatomy of some *Choricotyle* spp. and *Dactycotyle* spp., the differences lying in the presence in the latter of a very small and probably vestigial vagina and the absence of a corresponding structure in the former, and in the structure of the posterior adhesive organs. In *Dactycotyle* the posterior adhesive organs function in the manner of pincers, whereas in *Choricotyle* they act in the manner of reinforced acetabulate suckers. The presence of a posterior terminal languette, assumed to be a rudimentary hook-bearing appendage, in *Choricotyle chrysophryi*, *C. labracis*, and *Cyclobothrium sessilis*, and in *Dactycotyle minor*, is further evidence of a close affinity between the Choricotylidae and the Mazocriidae. This opinion is strengthened when the posterior muscular systems of *Choricotyle chrysophryi* and *Dactycotyle denticulata*, *D. merlangi*, and *D. minor* are compared. In all four of these Polyopisthocotylineans the respective muscular systems are identical. Thus we can conclude that the Choricotylidae are close relatives of some of the Mazocriidae, but bear less affinity with the Polystomidae, Onchocotylidae, and Microcotylidae.

VI. SUMMARY

1. The family Diclidophoridae Fuhrmann, 1928 has been revised, and the diagnosis of the replacing family Choricotylidae has been given.

2. Keys to the genera and species of the Choricotylidae have been constructed.

3. All species of the family have been reviewed and a diagnosis of each has been given.

4. Species previously referred to the genus *Diclidophora* have been transferred to the genus *Choricotyle*.

5. The following taxonomic changes have been proposed:

(*a*) *Choricotyle merlangi* (MacCallum, 1917) as a nom. nov. for the '*Diclidophora merlangi* Kuhn, 1829' described by MacCallum (1917).

(*b*) *Choricotyle charcoti* (Dollfus, 1922*a*, *b*) as a n.comb. to replace *Cyclobothrium charcoti* Dollfus, 1922.

(*c*) *Diclidophora* '*species*' Fuhrmann, 1928 as a synonym of *Choricotyle charcoti* (Dollfus, 1922*a*, *b*).

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THE TAXONOMY OF THE MONOGENETIC TREMATODE *PLECTANOCOTYLE GURNARDI* (v. BEN. & HESSE)

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(With 1 Figure in the Text)

Plectanocotyle gurnardi (v. Ben. & Hesse, 1863) n.comb.

syn. *Phyllocotyle gurnardi* v. Ben. & Hesse, 1863.
syn. *Plectanocotyle Lorenzii* Monticelli, 1899.
syn. *Plectanocotyle caudata* Lebour, 1908.

Specimens of *Plectanocotyle gurnardi* were obtained by the writer from the gills of *Trigla cuculus* L. and *T. gurnardus* L. during trawling operations at the Irish Atlantic Slope fishing grounds in August 1938 and July 1939. One specimen of *Plectanocotyle gurnardi* was collected from a *Trigla gurnardus* and seven specimens of the same parasite from eight specimens of *T. cuculus*, the greatest degree of infestation encountered being 3 parasites per host fish. *Plectanocotyle gurnardi* has been recorded previously, under one or other of the synonyms listed above, from *Trigla gurnardus* by van Beneden & Hesse (1863), T. Scott (1901, 1905), A. Scott (1904), Lebour (1908), and Little (1929); from *T. lucerna* L. by A. Scott & Little; and from *Trigla* 'sp.' by Monticelli (1899). It will be noted that the present records of the parasite are from its usual host *T. gurnardus* and from a new host *T. cuculus*.

The anatomy of *Plectanocotyle gurnardi* has been described in detail by Monticelli (1899), but there has been confusion as to the identity of the parasite. The genus *Plectanocotyle* was founded by Diesing (1850) with *P. elliptica* as the type species. Monticelli (1899) described a new species as *P. Lorenzii*, but this is clearly identical with *Phyllocotyle gurnardi* van Beneden & Hesse as described and figured by the founders of the latter species (1863) and by T. Scott (1901, 1905). Van Beneden & Hesse had created unnecessarily the new genus *Phyllocotyle* for *P. gurnardi*, whereas this species should have been included in the genus *Plectanocotyle* Diesing, 1850.

Monticelli founded *Plectanocotyle Lorenzii* without any reference to *Phyllocotyle* van Beneden & Hesse, 1863, and later (T. Scott, 1905) he identified personally a parasite recorded by Scott under the name of *Phyllocotyle gurnardi*, as *Plectanocotyle Lorenzii*. In carrying out this identification Monticelli apparently did not realise, or at any rate did not recognize, the priority of the specific name under which Scott had recorded the parasite. Again, Scott could not have consulted carefully the separate copy of Monticelli's description of *P. Lorenzii* to which he makes reference (1905), otherwise it is difficult to conceive how Scott could have assumed the difference between *Phyllocotyle* and *Plectanocotyle* to be the presence in the former of a posterior terminal

hook-bearing appendage, and the absence of such a structure in the latter. Monticelli (1899) had illustrated clearly the presence of a posterior hook-bearing appendage in *Plectanocotyle Lorenzii*, and furthermore, throughout the literature on the subject there is no illustration of any species of *Phyllocotyle* or of *Plectanocotyle* which does not bear this terminal appendage.

Lebour (1908) described a new species from the gills of *Trigla gurnardus* as *Plectanocotyle caudata*, but suggested that this new species and *P. Lorenzii* and *Phyllocotyle gurnardi* might all represent the same species in various degrees of contraction. Specimens in the possession of the writer represent degrees of contraction intermediate between those figured by Lebour for *Plectanocotyle caudata* and by Monticelli for *P. Lorenzii*. Further, Lebour stated that the anatomy of these animals differed very slightly, the only difference being in the armature of the posterior peduncle. *P. Lorenzii*, according to Monticelli, possessed two pairs of hooks on the posterior peduncle, but Lebour discovered, in *P. caudata*, a third pair of minute hooks in addition to the other two pairs identical with those in *P. Lorenzii*. In the material examined by the writer a pair of very small hooks comparable with the third pair in *P. caudata* is present in one specimen (Fig. 1 *c*), but it is impossible to distinguish them in other specimens. The writer has observed variations of a similar nature, i.e. of minute skeletal structures, in other undoubted members of the same species, e.g. the 'squellette' in *Dactycotyle merlangi*, and 'piece *f*' of the skeleton of the suckers of *Choricotyle chrysophryi* as described by the writer (1941). Thus it can be concluded with reasonable certainty that *Plectanocotyle caudata* Lebour, 1908 is a synonym of *Plectanocotyle gurnardi* (van Beneden & Hesse, 1863).

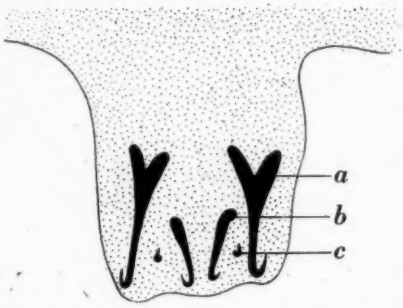

Fig. 1. *Plectanocotyle gurnardi*. Posterior hook-bearing peduncle in ventral view. *a*, *b*, *c*, hooks of the first, second, and third pairs respectively.

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THE SCOLEX OF *APORHYNCHUS NORVEGICUS* (OLSS.)

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(With 8 Figures in the Text)

The following is an account of the anatomy of the scolex of *Aporhynchus norvegicus* (Olss.) involving details of the musculature and nervous and excretory systems. The anatomy of the strobila has been described by Nybelin (1918). The specimens, mostly young complete strobilae, were obtained from the intestine of *Spinax spinax* caught in the deep-sea fishing grounds to the west of Ireland. Until recently the species had only been recorded from the coast of Norway, but in 1936 Joyeux & Baer found it in French waters. It was first described as *Tetrarhynchus norvegicus* by Olsson (1867), the genus *Aporhynchus* being created by Nybelin (1918) for the single species.

Specimens were fixed in Gilson's fluid immediately on removal from the host and subsequently stored in 70% alcohol until brought to the laboratory. Transverse and longitudinal sections have been cut at 5μ and stained with Delafield's haematoxylin and eosin or orange G.

The scolex is 1·5–1·8 mm. long and 0·8 mm. broad; it bears two dorsal and two ventral bothridia. The bothridia, in fixed specimens, are oval, 0·55 mm. × 0·35 mm., the posterior border being better defined than the anterior (Fig. 1). Olsson (1867) has described the extreme mobility of the scolex and bothridia in living specimens. The entire surface of the scolex and of the bothridia is armed with small backwardly directed spines; there are no proboscides but at the apex of the scolex open the ducts of unicellular glands situated just behind the bothridia. Following the scolex is an unsegmented region of the strobila 0·6 mm. long.

Musculature

The musculature of the posterior region of the scolex is the same as that of the strobila, consisting mainly of the superficial system of outer circular and inner longitudinal muscles. The circular muscles lie immediately below the basement membrane and the longitudinal within these. The latter are arranged in small bundles, the fibres of which anastomose with those from neighbouring bundles. There is no inner system of circular muscles dividing the parenchyma into cortical and medullary regions, but a few scattered bundles of longitudinal fibres occur laterally in the region of the excretory vessels and lateral nerve cords. The sagittal muscles which in the majority of cestodes occur in the cortical parenchyma are here replaced by dorso-ventral muscles which extend across the body being better developed laterally; they are in the form of delicate apparently single fibres.

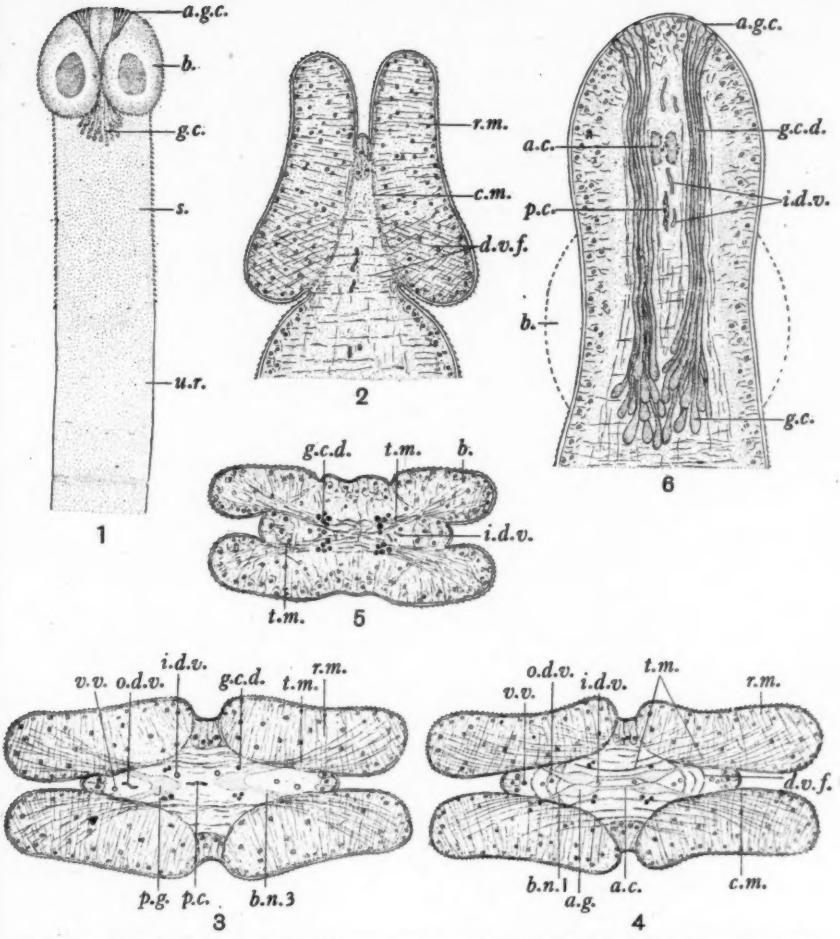
Anteriorly the bothridia constitute the main muscle mass of the scolex. Each bothridium is limited on its inner side by a well-defined layer of circular muscle fibres (Figs. 2, 4), which are continued right round the bothridium, being more delicate on the outer side where they lie just below the cuticle and basement membrane lining the cavity. At their anterior extremities the inner borders of the bothridia are not so sharply demarcated (Fig. 5). A very delicate layer of longitudinal fibres lies within the circular, both on the inner and outer sides of each bothridium, but they are very poorly developed and only faintly visible in longitudinal sections (Fig. 2). The main mass of each bothridium is made up of radial muscles. In addition the two dorsal and two ventral bothridia are connected to one another by transverse muscle fibres (Figs. 3–5). These are best apparent anteriorly where a band of muscles runs transversely across the scolex connecting the right and left dorsal, and the right and left ventral bothridia (Fig. 5). In the centre the dorsal and ventral transverse fibres are more or less contiguous while laterally they separate so that the whole arrangement is X-shaped. The fibres branch and spread out at their extremities where they enter the bothridia and cross the radial muscles obliquely to terminate near the outer margins. These transverse muscles are still visible as far back as the brain though they are not so strongly developed. When the bothridia are better determined on their inner borders these transverse fibres are mainly confined to the small intervening space dorsally and ventrally; some of the fibres still extend into the bothridia passing obliquely outwards (Figs. 3, 4). Behind the brain the transverse fibres gradually disappear and the dorso-ventral fibres become more apparent. They extend between the dorsal and ventral bothridia of the right and left sides respectively, passing into them to pursue a slightly backward course (Fig. 2).

In the restricted areas of the scolex laterally and dorsally between the bothridia the muscles are feebly developed and of the superficial type, these areas are occupied mainly by large cells of, possibly, a glandular nature. The gland cells proper of the scolex form a club-shaped mass of unicellular structures situated just behind the posterior margins of the bothridia. The ducts from these run forwards dorsally and ventrally to the brain and commissures (Figs. 3–6) to open by a series of pores at the apex of the scolex (Fig. 1). Possibly these have an adhesive function and act as a substitute for the proboscides of other Tetrarhynchs.

Nervous system

The nervous system (Figs. 7, 8) consists of a brain, two lateral nerve cords, anterior nerves arising from the brain and supplying the anterior extremity of the scolex, and bothridial nerves, arising some from the brain and some from the lateral nerve cords, supplying the bothridia.

Brain. The brain is situated near the anterior end of the scolex, its posterior limit being on a level with the centre of the bothridia (Fig. 7). It is compressed dorso-ventrally and consists of two pairs of ganglia dorsally and two ventrally, one pair being anterior and the other posterior. The anterior ganglia are shaped



Figs. 1–6. *Aporhynchus norvegicus*. All drawings are semi-diagrammatic and have been simplified for clarity. *a.c.* anterior commissure; *a.g.* anterior ganglion; *a.g.c.* aperture of gland cell; *a.v.d.v.* anastomosis of ventral and dorsal excretory vessels; *a.d.v.* anastomosis of inner and outer dorsal excretory vessels; *b.* bothridium; *b.n.* bothridial nerves 1–6; *c.m.* circular muscles; *d.v.* dorsal excretory vessel; *d.v.f.* dorso-ventral fibres; *e.* excretory vessels to bothridia; *g.c.* gland cell; *g.c.d.* duct from gland cell; *i.a.n.* inner anterior nerve; *i.d.v.* inner branch of dorsal excretory vessel; *l.b.n.* longitudinal bothridial nerve; *n.c.* nerve cord; *o.a.n.* outer anterior nerve; *o.d.v.* outer branch of dorsal excretory vessel; *p.c.* posterior commissure; *p.g.* posterior ganglion; *r.m.* radial muscles; *s.* scolex; *t.m.* transverse muscles; *u.r.* unsegmented region following scolex; *v.v.* ventral excretory vessel.

Fig. 1. Scolex, dorsal view. The spines are represented around the margin only but actually cover the entire surface of scolex and bothridia.

Fig. 2. Transverse section through bothridia and posterior ganglia.

Fig. 3. Transverse section through bothridia and anterior ganglia and commissures.

Fig. 5. Transverse section through anterior extremity of scolex.

Fig. 6. Median tangential longitudinal section through scolex showing commissures and glands.

like a biconvex lens being rounded in surface view and oval in transverse section (Figs. 3, 4). The two dorsal and two ventral anterior ganglia are connected by transverse anterior commissures which pass parallel to one another across the middle of the scolex (Figs. 4, 6, 7). Each anterior ganglion is continuous behind with a posterior ganglion and the dorsal and ventral posterior ganglia of each side fuse to form a single ganglionic mass (Figs. 3, 8) which is

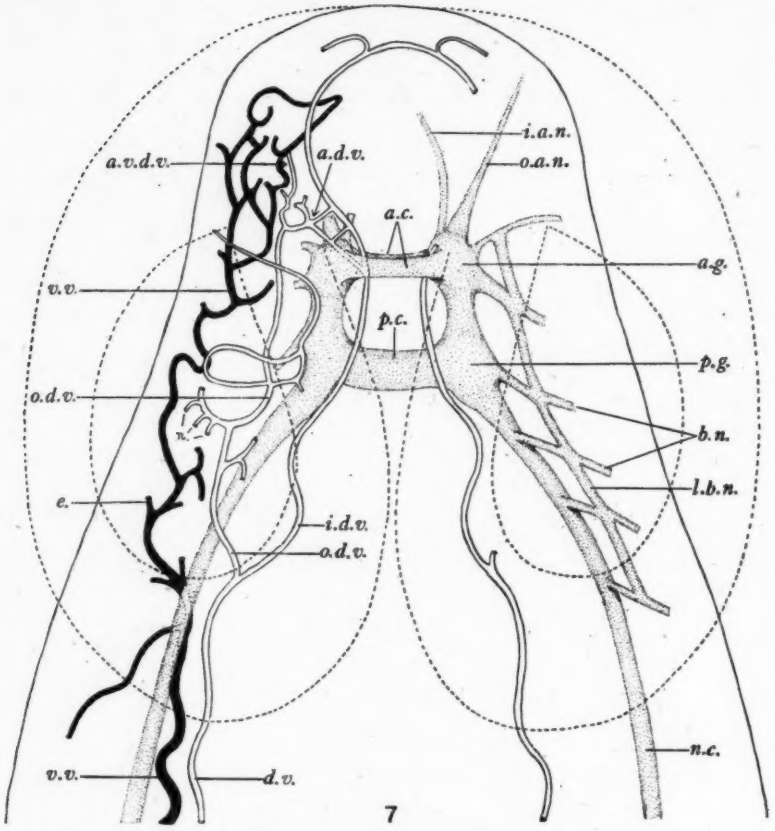


Fig. 7. *Aporhynchus norvegicus.* Scolex showing, on the right, the dorsal half of the nervous system and, on the left, the dorsal and ventral excretory vessels.

connected to its partner of the opposite side by a median posterior commissure which runs parallel to and a little distance behind the anterior commissures (Figs. 6, 7). As in *Grillotia erinacea* (Johnstone, 1911) and *Dibothriorhynchus grossum* (Rees, 1941) the so-called ganglia do not contain nerve cells but consist of a tissue which seems to be composed of fine fibres arranged in a network enclosing small spaces. The posterior median commissure is the only part of

the nervous system in which ganglion cells have been found to occur. The ganglia and commissures are bounded by a delicate limiting layer which contains a number of nuclei (Fig. 6) especially around the roots of the nerves.

Lateral nerve cords. The lateral nerve cords arise one from each pair of fused posterior ganglia. From their points of origin they extend obliquely outwards towards the lateral margins of the scolex and continue throughout the whole length of the strobila to its posterior extremity.

Anterior nerves. An outer and an inner anterior nerve arise from the anterior end of each anterior ganglion so that there are two right and two left dorsal, and two right and two left ventral nerves (Figs. 7, 8). The inner anterior nerves are fairly short, they curve inwards to supply the central part of the anterior region of the scolex. The outer anterior nerves pass obliquely outwards to supply the antero-lateral region in front of the bothridia; no branching of these nerves has been observed.

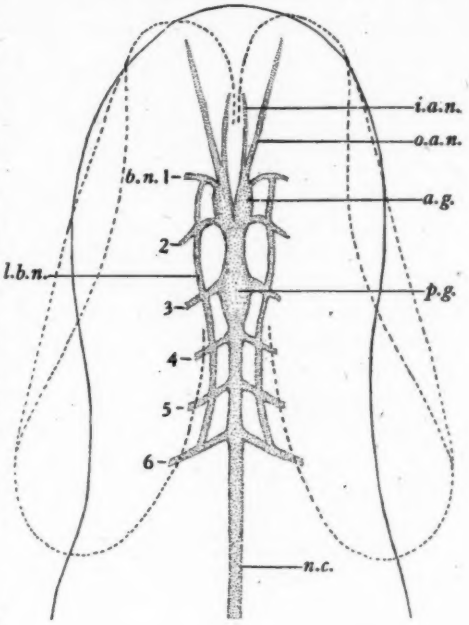


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Fig. 8. *Aporhynchus norvegicus.* Lateral view of brain and nerve cord showing origin of dorsal and ventral anterior and bothridial nerves of one side.

Bothridial nerves. Each bothridium is supplied with six nerves more or less evenly distributed along its length (Figs. 7, 8). The first three nerves in each case arise from the brain dorsally and ventrally and the remaining three in pairs from each lateral nerve cord. Of the three arising from the brain the first two arise from the anterior ganglia, two dorsally and two ventrally on either side (Figs. 4, 7, 8). The two dorsal enter the dorsal bothridium and the two ventral the ventral bothridium of its own side. The third bothridial nerve arises from the fused posterior ganglia, one dorsally and the other ventrally on each side. They pass postero-dorsally and postero-ventrally to enter their respective bothridia (Figs. 3, 7, 8). The remaining bothridial nerves arise in three pairs from the early part of each lateral nerve cord (Figs. 7, 8). All six bothridial nerves are more or less evenly spaced, and each series is joined together by a longitudinal bothridial nerve before entering the bothridia. There are therefore two dorsal and two ventral longitudinal bothridial nerves

which extend from the first bothridial nerve near its origin obliquely backwards to the sixth bothridial nerve (Figs. 7, 8).

No nerves supplying other parts of the scolex have been found. The greater part is occupied by the bothridia, the areas between being much restricted and apparently devoid of an independent nerve supply. Due to the absence of proboscides the proboscis nerves of other Tetrarhynchs are not present. Otherwise the nervous system shows a similarity in general principles to that of *Grillotia erinacea* and *Dibothriorhynchus grossum*.

Excretory system

A dorsal and a ventral excretory vessel extend throughout the body on either side, the dorsal vessel is smaller in diameter than the ventral and lies slightly within it (Fig. 7). In the scolex the excretory system is complicated by the branching of these vessels. Just in front of the posterior margins of the bothridia the vessels begin to branch. The dorsal vessel on each side divides into an inner and an outer branch (Fig. 7). The inner branch extends forwards and inwards passing dorsally to the median posterior commissure and then on between the dorsal and ventral anterior commissures towards the anterior extremity (Figs. 3, 4, 6, 7). Having passed between these commissures the two vessels loop outwards and then turn in again so that the right and left meet and fuse in the middle line near the apex of the scolex (Fig. 7). The outer branch of each dorsal vessel does not pass through the nerve ring but is confined to the lateral region of the scolex between the dorsal and ventral bothridia of each side (Figs. 3, 4). Here too lies the whole of the ventral vessel (Fig. 7). Both the ventral vessel and the outer branch of the dorsal are much branched and tend in places to form a network. The outer and inner branches of the dorsal vessel anastomose with one another just as the latter emerges from the nerve ring, and there is also in this region an anastomosis between the dorsal and ventral vessels. From these vessels on either side arise branches which enter the bothridia dorsally and ventrally. It was impossible to trace the complicated network of vessels within the bothridia themselves.

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THE METACERCARIA OF A PLEUROLOPHOCERCA CERCARIA PARASITIZING *PERINGIA ULVAE* (PENNANT, 1777)

By MIRIAM ROTHSCHILD

(With 4 Figures in the Text)

Introduction

The metacercaria shown in Fig. 1 was obtained in the laboratory from Gobies (*Gobius ruthensparri* Euphras.) experimentally infected with a Pleurolophocerca cercaria from *Peringia ulvae*. This cercaria[1] is regarded as the most interesting of all the Heterophyid larvae infecting this snail. It has been referred to briefly in a previous publication (Rothschild, 1938). It differs from typical Opisthorchid cercariae in the following characteristics:

(1) The lateral fin-folds are continuous and extend the whole length of the tail. The dorso-ventral fin-fold is reduced.

(2) The oesophagus and intestinal caeca (in addition to the pharynx) can be clearly made out.

(3) The cuticle is more heavily spined.

(4) The ventral sucker is better developed.

(5) The penetration gland ducts (fourteen in number) are not arranged in such definite bundles.

(6) Three acicular boring spines are present in the oral sucker.

In other respects the cercaria possesses the usual characters of the group.

Great store was set by the solution of the life history of this species, as the author thought that the adult would prove to pertain to the subfamily Haplorchiinae Looss, 1899. Attempts were made over a period of 6 years but without success.

Life-history experiments

These cercariae have a very definite distribution in the first intermediate host, a fact which generally greatly facilitates the discovery of the final host. *P. ulvae* is found in greatest numbers on the estuarine mud-flats, but is also present in the roots of the vegetation and in pools throughout the saltings (Rothschild, 1941). These cercariae, however, are only very rarely found in *P. ulvae* from the mud-flats proper, but on the other hand form a large proportion of the infections in pools round the periphery of the saltings. It has been pointed out elsewhere that the percentage of infection of all Pleurolophocerca cercariae is lower on the mud-flats than in pools. Cryptocotyle cercariae, however, occur more frequently there than these supposed Haplorchis

[1] Although only one species is referred to here, several almost indistinguishable species were found in *P. ulvae*, all of which used the same second intermediate host.

cercariae, but in the pools their numbers, though fluctuating, remain more or less equal.

This fact immediately suggests that the final host is also most commonly met with round the periphery of the saltings. Conditions in the pools are more extreme and might well provide an ecological barrier to certain species which can survive on the mud-flats, but the reverse is unlikely to be true. The key to this type of distribution is almost always to be found in the movements of the final host.

The pools in which the 'Haplorchid' cercariae are most common are those high up along the edge of the saltings, which are only covered briefly at high or spring tides. This observation applies to the Camel, in addition to the Tamar Estuary.

The briefest survey of these pools convinced the author that the final host of this trematode could not be a fish. Apart from a few gobies no fish were present in them. Yet in tiny pools, only covered by the tide for a relatively short period each month, the infection rate with these cercariae sometimes reached 21 % of all snails of 3 mm. and over in length. To bring about this very high rate the snails would have to be continually exposed to the attack of the miracidia. It is inconceivable that during spring tides infected fish in sufficient numbers to fulfil this requirement could swim up the estuaries and over the saltings. Even far out on the mud-flats, which are daily covered by the tides, the infection rate of *P. ulvae* with cercariae of fish parasites is consistently low —as indeed it is for all species of trematode larvae in snails obtained from large expanses of open water.

In the absence of Amphibia and mammals from this region it was considered certain that the final host was a bird—a view still cherished by the author despite the failure to prove it experimentally.

Gobies were clearly indicated as the second intermediate host. This surmise proved to be correct. The cercariae readily penetrated the fins and skin where they encysted.

The search then appeared to be narrowed down to some common fish eating bird. The fact that no Haplorchid or related fluke had been recovered frequently from British estuarine birds is not of much significance. The relatively scanty records of *Cryptocotyle jejuna* Nicoll, for example, can in no way give a true picture of the occurrence of this fluke, which is certainly both common and widely distributed.

Experiments were carried out with laboratory-reared chickens, ducks, herring gulls, black-headed gulls and one redshank. All proved negative. On the ninth day after feeding a few Heterophyid eggs were recovered from the faeces of one of the black-headed gulls, but on dissection no fluke was found.

The redshank (*Tringa totanus* L.) had always been considered the most likely host directly it was realized how eagerly this bird fed on small fish. It was, however, difficult to obtain laboratory-reared redshanks until 1940. Eight days after the feeding experiments commenced the redshank was killed

by blast from a high-explosive bomb. A dissection was made immediately after death, but not a single excysted metacercaria or immature fluke was found.

Many variations of these feeding experiments were tried. The diet of the final host was changed and all vitamins omitted. The birds were also starved before feeding.

The infected gobies, still alive, were fed at all stages after exposure to the attack of the cercariae, ranging from a few hours[1] up to 3 months after infection.

The metacercariae seem to reach maximum size at about 3 weeks of age, and were still alive after 3 months. At no period, however, did they display much activity when released from the cyst, and the cyst wall broke down easily when teased with dissecting needles. It seemed possible, in view of the observations made on the metacercaria of *C. lingua* in the laboratory (Rothschild, 1941 *b*), that the failure of the experiments was due to a poor condition of the metacercaria rather than a wrong choice of final host. With this in mind an attempt was made to vary the conditions under which the gobies were kept. The tanks at the Laboratory at Plymouth contain sea water in circulation, and although the gobies live healthily in such tanks, it was realized that in nature they seek brackish water rather than pure sea water. Accordingly, a new set of experiments was made, in which the gobies were kept in water of varying salinities, and also at varying temperatures. All these experiments were equally unsuccessful.

Various other fish were then tried as intermediate hosts, but although a few cercariae attempted penetration in rockling (*Onos* spp.), it was obvious that these hosts were not attractive to them and no results were obtained.

It would be now worth while collecting naturally infected gobies and attempting feeding experiments along the lines indicated above, but unfortunately, owing to the war, the study of this interesting life history has been abandoned.

THE CYST AND METACERCARIA

The cyst (Fig. 4). A goby was placed in a finger bowl containing brackish water together with seventeen specimens of *Peringia ulvae* infected with the 'Haplorchid' cercariae. At the end of 3 weeks the fish was killed. The whole skin, including the surface of the eyes, contained cysts. In one pectoral fin, 670, of varying age and size, were counted. No pigment marked the site of the cyst, but an opaque whitish area surrounded some of those situated in the fins.

The cysts when fully developed, distinctly protrude from the surface of the host's skin. They are roughly circular or slightly oblong, with a stout, hyaline

[1] Most Heterophyid cysts become viable only after about 14 days in the second intermediate host. Metacercariae which are viable almost immediately after encystment are generally those which use short lived animals, such as insects, as the second intermediate host. Gobies, however, appear to be annuals and their death in the Laboratory during May and June always restricted the experiments to the autumn and winter.

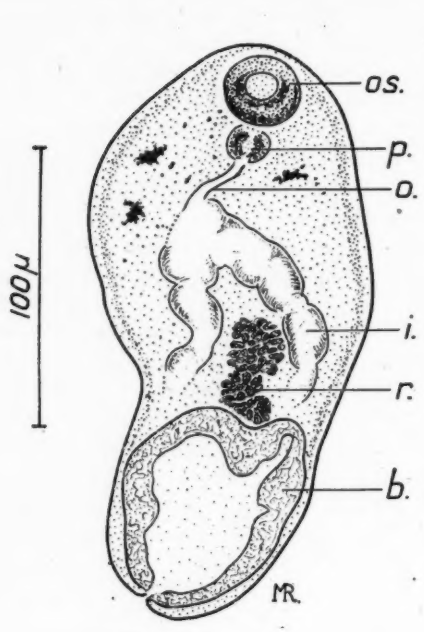

Fig. 1.

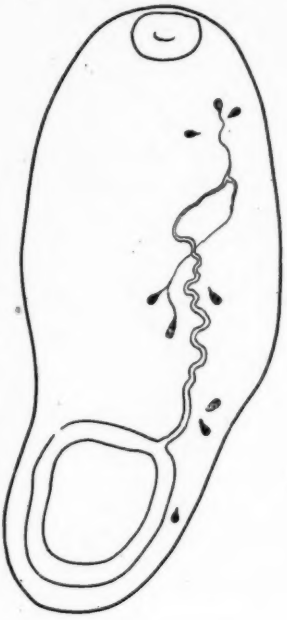

Fig. 2.

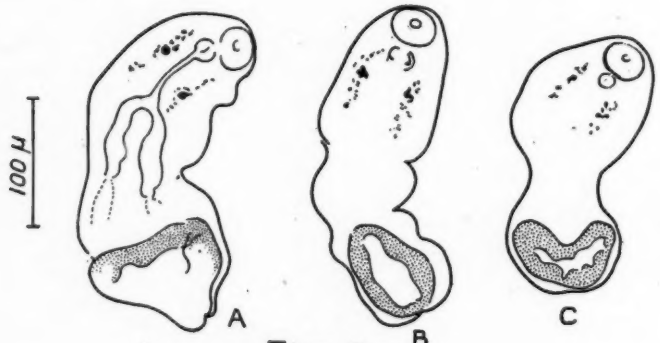

Fig. 3.

Fig. 1. Diagram of excysted metacercaria from experimentally infected goby (drawn rom a preserved specimen). *b*, bladder; *i*, intestine; *o*, oesophagus; *os*, oral sucker; *p*, pharynx; *r*, Anlage of reproductive organs.

Fig. 2. Excretory system of metacercaria.

Fig. 3. Excysted, living metacercariae (camera lucida drawings).

inner wall, and a weaker, less well defined outer wall. A maximum sized cyst measures roughly 180 μ in diameter. Encapsuled worms measure from 113 to 130 μ in diameter when fully grown.

The metacercaria (Figs. 1–3). The largest excysted metacercaria obtained (Fig. 1) was fixed in Bouin Duboscq and stained with Delafield's haematoxylin. The measurements are as follows: length of body 201 μ, width of body (maximum) 101 μ, oral sucker 28 × 24 μ, pharynx 14 × 12 μ, oesophagus (length) 10 μ, distance between eye spots 35 μ.

As already stated the metacercariae were sluggish, apparently almost moribund, and tended to remain folded when released from their cysts. The most conspicuous features are: (1) rather voluminous intestinal caeca (the terminal portions of which could not be made out) which contrast with a very narrow oesophagus. (2) The single, centrally situated, dark mass of cells, which

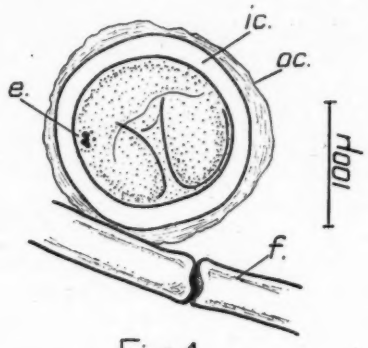

Fig. 4

Fig. 4. Diagram of cyst from the fin of experimentally infected goby. *e*, eye-spots; *f*, fin ray of host; *ic*, inner cyst wall; *oc*, outer cyst wall;

represents the Anlage of the reproductive organs. (3) The large bladder with enormously thick walls. (4) The remains of the pigmented eye-spots.

The excretory system was difficult to trace. The main collecting tubes were eventually seen, as shown in Fig. 2. They are of a typical heterophyid type, passing forward until they reach about the level of the eye-spots, where they divide into a small anterior branch and a larger posterior branch. There appears to be one group of three flame-cells attached to the anterior branch, and two groups of three attached to the posterior branch. As no more than three flame-cells were seen in the same specimen it is difficult to be sure of the groups. The excretory pore is terminal.

The cuticular spines were much less conspicuous in the metacercariae than in the cercariae.

From a glance at Fig. 1 it will be realized that the various organs of this metacercaria, particularly the testes, are not sufficiently developed to enable one to assign it with confidence to any special group. The intestine is, however,

of the Haplorchis type, and what evidence can be gathered from the position of the reproductive organs speaks in favour of the species pertaining to the Haplorchiinae.

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ON *STYPHLODORA ELEGANS* N.SP. AND *STYPHLODORA COMPACTUM* N.SP., TREMATODE PARASITES OF *PYTHON RETICULATUS* IN MALAYA, WITH A KEY TO THE SPECIES OF THE GENUS *STYPHLODORA* LOOSS, 1899

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(With 3 Figures in the Text)

Numerous specimens of a trematode which has proved to be a new species were collected from the kidneys of 'Ular sawa' (*Python reticulatus*) at Alor Star and at Kedah, Malaya, by Mr G. B. Purvis, F.R.C.V.S. One batch comprises about 350 specimens, another one more than 150, and the entire collection of five batches exceeds 600 specimens. For this new species the name *Styphlodora elegans* is proposed. Mr Purvis also collected a single specimen of what seems to be a second new species from the stomach of the python at Alor Star, and for this the name *Styphlodora compactum* is proposed. Type specimens of the two new species are lodged in the British Museum (Natural History), London.

This paper is devoted to descriptions of the new species, but some consideration has also been given to the relation between the sizes and dispositions of certain organs and the length of the body in fifty specimens of *S. elegans* which cover a considerable range of sizes. Justification for this lies in the fact that very little is known about the proportions of parts of the body in relation to growth in the Trematoda, so that difficulties arise when two or more species are compared because total size varies and because growth changes are not understood. It is important to realize that the proportions of the individuals of a species may vary for no other reason than that their total sizes are different. The writer has determined that the proportions of *S. elegans* vary in relation to total size and has devised a method of plotting measurements which, if consistently applied whenever numerous specimens of a species are available, could reduce the systematist's difficulties by resolving systematic units more clearly. The writer has also concerned himself with a criticism of the only existing key to the species of *Styphlodora* and has provided an alternative key.

Styphlodora elegans n.sp.

Most specimens are 4–6 mm. long and 1·0–1·5 mm. in maximum breadth. There are many smaller specimens, some less than 2 mm. long, with numerous egg capsules in the uterus. The delicate appearance is due to the thinness of the

cuticle and the fine nature of the parenchyma. Through these layers all the important organs can be seen even in uncleared specimens which have been stored in alcohol for several years. Observations were made, however, on specimens stained and mounted.

Delicate spines, 0·013–0·014 mm. long, are set in regular transverse and fairly regular longitudinal rows in the cuticle. The transverse rows are about 0·014 mm. apart and the longitudinal rows are so closely set that clusters of two or three spines are evident at regular intervals along the margins of the body. In some specimens the transverse rows of spines terminate at the level of the posterior testis. Farther back there are only fine spicular bodies which seem to be abraded spines. The living animal must have a complete covering of spines, because some individuals show this character, although spines may be entirely lacking. This evidence partially justifies Nicoll's assumption (1912) that spines exist, although they were not actually seen in *S. najae*. The spines are probably much finer, however, than those tentatively drawn in Nicoll's Fig. 122 A.

The oval mouth is situated on the ventral side of the anterior tip of the body, and the encircling oral sucker is almost spherical but slightly flattened posteriorly. The unarmed ventral sucker, which is larger than the oral one, extends slightly beyond the limit of the anterior one-third of the body length. The common genital pore, from which a well-developed cirrus protrudes in many specimens, is situated well in front of the ventral sucker and slightly to the left of the median plane. Behind the mouth there is a short but definite prepharynx, which is typically longer than the pharynx but shorter than the oesophagus (Fig. 1 A). The pharynx lacks 'teeth' and is broader than long. At its base there is a cluster of cellular gland-like bodies which are perhaps related functionally to the oesophagus. The bifurcation of the gut occurs immediately in front of the genital pore and the caeca, which terminate in the middle of the posterior third of the body. In some specimens the right caecum is slightly longer than the left one.

The anterior and posterior testes, which are circular or oval, are situated respectively in front of and behind the mid-point of the body, the anterior one to the left and the posterior one to the right of the median plane. Irregularity of contour is uncommon, indented margins occurring in only nine out of more than sixty specimens examined. The posterior testis is almost invariably slightly larger than the anterior one. The relative positions of the testes vary slightly. In fifty-one specimens there is considerable overlap at about the mid-point of the body, in nine others there is little or no such overlap, and in three others the testes lie almost side by side. The degree of obliquity of the testes is thus a less reliable criterion of specific distinction than Bhalerao (1936) supposed for other species.

Vasa efferentia traverse only a short region of the body before uniting to form a vas deferens near the base of the male organ which is an unarmed cirrus of considerable length. The ductus ejaculatorius is narrow generally, but in

some specimens it is dilated to half the breadth of the cirrus. It shows slight sinuosities but no definite folding and it widens posteriorly into a long, oval, seminal vesicle which often shows a central constriction and consequently has an hour-glass shape. Prostate glands border the ejaculatory duct. All the

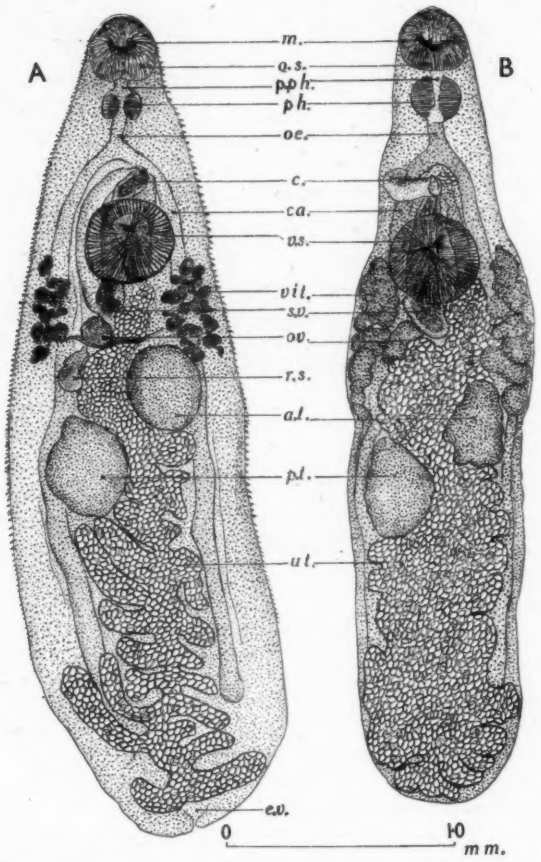

Fig. 1. A, *Styphlodora elegans* n.sp.; B, *Styphlodora compactum* n.sp., both shown in ventral view. *a.t.* anterior testis; *c.* cirrus; *ca.* caeca; *e.v.* excretory vesicle; *m.* mouth; *oe.* oesophagus; *o.s.* oral sucker; *ov.* ovary; *ph.* pharynx; *p.ph.* prepharynx; *p.t.* posterior testis; *r.s.* receptaculum seminis; *s.v.* seminal vesicle; *ut.* uterus; *vit.* vitellaria; *v.s.* ventral sucker.

terminal parts of the male apparatus are housed in a large cirrus sac, so that a vesicula seminalis externa is lacking.

The ovary, which is very much smaller than the testes, is situated in front of the posterior testis and thus to the right of the median plane. It is almost spherical. In the parenchyma behind the ovary but in front of the posterior

testis there is a large oval receptaculum seminis, which is at least as large as the ovary and may be larger. It is usually crowded with spermatozoa.

Much of the median field of the body is occupied by the uterus, which is crowded with operculate egg capsules in even the smallest specimens. The metraterm is not notably muscular, so that it is inconspicuous in some specimens. It joins the uterus above the mid-point of the ventral sucker. The terminal part of the uterus lies to the left of the median plane and crosses this in winding round the anterior testis. In this situation the uterus is only slightly folded and between the testes the folds are suppressed, but behind the testes large loops of the uterus extend to the inner margins of the caeca. Behind the terminations of the caeca the loops are not restricted to the median field of the body but sweep outwards and slightly forwards almost to its lateral margins. The number of uterine folds posterior to the testes varies from about eight in small specimens to eleven or twelve in large ones. Some of these folds are on the recurrent limb of the uterus, which ends in the oötype. This is situated near the median plane immediately to the left of the ovary. Shell glands are inconspicuous, so that the oötype can be made out only by the clear space it provides and by the junction of the main vitelloducts, which cross the posterior border of the ovary.

Both the main vitelloducts and their factors are crowded with vacuolated 'yolk-cells' which, as in other trematodes, carry their microscopic droplets of shell-forming material to the oötype (see Dawes, 1940). The cells originate in the vitellaria, which comprise about a dozen clusters of follicles, small and well defined, in each lateral field of the body. They extend from about the middle of the anterior testis to the posterior margin of the ventral sucker. They are generally asymmetrical, extending farther back on the right side than on the left. In fifteen specimens out of sixty-four they reach back to the posterior testis.

When we consider that the oötype, which serves as a mould for the developing egg capsule, might grow like the rest of the body, it seems unlikely that the eggs of large and small specimens will be of constant size. Measurements reveal a fair degree of constancy, however. The mean sizes of ten of the eggs of specimens respectively 2·1, 4·2 and 6·1 mm. long are $0{\cdot}037 \times 0{\cdot}022$, $0{\cdot}043 \times 0{\cdot}019$ and $0{\cdot}041 \times 0{\cdot}019$ mm. The greater length and smaller breadth of the eggs of larger individuals may be due to greater lateral compression in a more crowded uterus. We may conclude that the oötype, which determines the size of the egg capsule, does not vary in size proportionately with the body as a whole. It would be interesting to know if this holds good for all trematodes.

The excretory system is obscured in this trematode by the presence in the uterus of abundant eggs, but there is no reason to suppose that it differs significantly from that of most other species of the genus. The excretory pore is terminal.

S. elegans (Fig. 1 A) seems to be more closely related to *S. serrata* Looss, 1899 and *S. renalis* Tubangui, 1933 than to other species of the genus.

Accordingly, measurements of various organs and parts may be presented along with other data in comparing and contrasting the three species (Table 1). Points of variance are to be seen in regard to several characters, notably the form of the body, the relative size and position of the ventral sucker, the nature of the anterior end of the gut, the shapes and sizes of the testes, the presence or absence of folds of the uterus between the testes, and the size of the eggs. Such differences clearly indicate the validity of the new species which, in many respects, may be deemed to hold an intermediate systematic position between *S. serrata* and *S. renalis*.

Table 1

	S. renalis	*S. serrata*	*S. elegans*
Length of body (mm.)	2·3–4·6	2·7	1·9–5·6
Max. breadth (mm.)	0·95–1·7	0·8	0·43–1·4
Dia. oral sucker (mm.)	0·18–0·24 × 0·20–0·28	0·17	0·14–0·34
Dia. ventral sucker (mm.)	0·22–0·38 × 0·26–0·40	0·18–0·19	0·19–0·57
Ratios:			
Max. breadth/body length	0·41–0·37	0·30	0·23–0·25
Oral sucker/body length	0·08–0·05 × 0·21–0·16	0·06	0·07–0·06
Ventral sucker/body length	0·10–0·08 × 0·27–0·24	0·07	0·10–0·10
Position of ventral sucker	middle of anterior one-third of body	one-third body length from oral sucker	posterior part of anterior third of body
Size of pharynx (mm.)	0·14–0·20 × 0·10–0·16	'kräftig'	0·07–0·23 dia.
Prepharynx	lacking	present, small	present, larger
Oesophagus	'practically absent'	short	longer than pharynx
Genital pore	immediately anterior to ventral sucker	immediately anterior to ventral sucker	well in front of ventral sucker, at gut fork
Cirrus sac (length mm.)	0·40–0·64 × 0·14–0·20	short	0·24–0·89 × 0·07–0·34
Testes (form)	round-oval, indented, 2–5 lobes	irregularly oval, curved borders	round-oval, smooth contours
Testes (size, mm.)	0·34–0·52 × 0·17–0·35	?	(anterior) 0·27–0·51 × 0·23–0·60 (posterior) 0·30–0·71 × 0·21–0·57
Space between testes	wide	wide	narrow
Ovary (size, mm.)	0·20–0·24 × 0·18–0·19	?	0·14–0·28 dia.
Oötype	between ovary and anterior testis	between ovary and anterior testis	between ovary and posterior testis
Caeca reach to	posterior third of body	middle of posterior third of body	middle of posterior third of body
Extent of vitellaria	ventral sucker to anterior testis	middle ventral sucker to middle anterior testis	ventral sucker to anterior testis
Folds of uterus between testes?	present	present	lacking
Size of eggs:			
Length, mm.	0·045–0·048	0·042–0·046	0·037–0·043
Breadth, mm.	0·021–0·023	0·021	0·019–0·022

THE RELATION BETWEEN THE SIZES OF CERTAIN ORGANS AND THE SIZE OF THE ENTIRE BODY IN *S. ELEGANS*

The relative sizes and positions in the body of certain organs in specimens of different total size were determined in the following way. Camera lucida drawings representing a magnification of 35 diameters were prepared for fifty specimens which were selected at random. The outlines of certain organs

appropriate for measurement (oral sucker, ventral sucker, ovary and testes) were drawn in. Each drawing was then treated separately. The median line of the body was drawn in and both anterior and posterior boundaries of the organs were projected upon it. This facilitated not only measuring the organ's length but also defining its precise longitudinal position in the body. Measurements were plotted as shown in Fig. 2, from which the ovary has been deleted in the interests of legibility. This organ consistently occupies a position slightly in

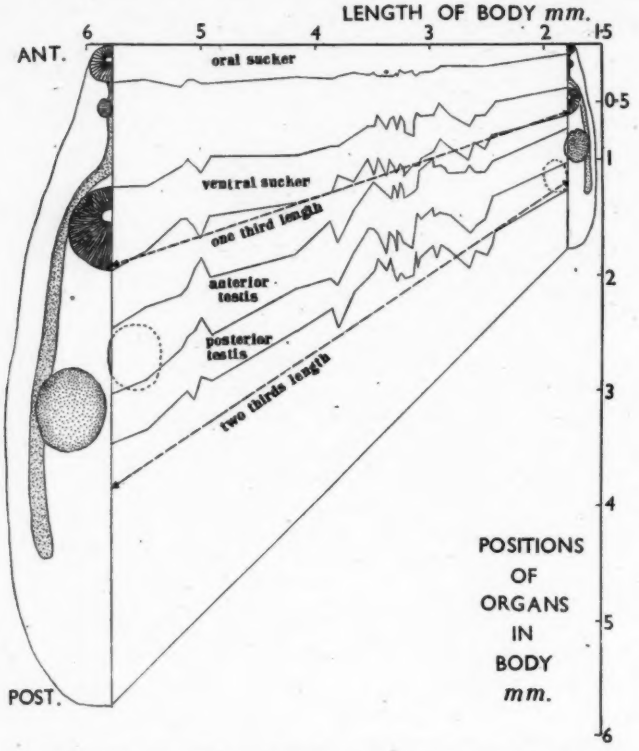

Fig. 2. Graph of measurements and positions of specified organs in fifty specimens of *S. elegans* taken at random.

front of the anterior testis. In the figure broken lines represent the levels at which the body may be divided into anterior, middle and posterior one-thirds. Measurements were also arranged in size classes, and Table 2 shows the results of defining the sizes of the organs as percentages of body length. This permits us to see at a glance the *relative* sizes of the organs.

The results indicate clearly that the relative sizes of the organs and the positions of the organs in the body are not constant but vary in individuals of different total size. The ventral sucker is of relatively smaller size the larger the

body as a whole, and vice versa (Table 2). Moreover, a relatively greater space must exist between the oral and ventral suckers in large individuals than in small ones, because the posterior margin of the ventral sucker is constant at about the junction of anterior and middle one-thirds of the body (Fig. 2). The gonads also become progressively relatively smaller with increase in size of the body, and although they maintain their positions relative to one another the relative shrinkage is more marked posteriorly than anteriorly. In a large individual more space (absolute and relative) is available in both anterior and posterior parts of the middle one-third of the body than is available in a small individual. This additional space accommodates the enlarging uterus which, as direct observations show, increases the number of its folds as well as its burden of eggs while the gonads are retrogressing in relative size and while the body is increasing in absolute size.

Table 2

Group	No. of specimens	Mean length mm.	Relative size of organ (percentage body length)				
			Oral sucker	Ventral sucker	Ovary	Anterior testis	Posterior testis
1	1	1·8	6·4	12·7	6·4	17·5	17·5
2	2	2·5	6·9	14·9	6·9	13·8	16·1
3	11	2·9	8·0	11·5	6·0	13·0	15·5
4	15	3·3	7·8	11·3	5·2	12·2	12·2
5	7	3·5	7·3	10·6	5·7	10·6	12·2
6	3	3·9	7·2	10·1	5·1	10·1	10·1
7	7	5·0	6·6	10·9	5·7	9·2	9·8
8	3	5·3	6·5	8·6	4·9	9·7	9·7
9	1	5·8	5·9	7·9	4·5	9·9	10·9
Weighted mean	50	3·8	7·4	11·1	5·6	11·6	12·6

It follows from these observations that even careful scrutiny of the sizes and dispositions of important organs in individuals of this species would reveal considerable differences if the individuals differed markedly in total size. Such differences, which might suggest specific distinction, represent only changes inherent in the processes of growth. It follows also that such changes must be taken into consideration whenever possible by systematists who are called upon to deal with other Trematoda.

Styphlodora compactum n.sp.

This species is proposed for the reception of the solitary trematode which Mr Purvis found in the stomach of a python at Alor Star, Malaya. It shows considerable differences from *S. elegans*, and the specific name has been chosen to signify a character in which it differs from all other species of the genus, namely, the degree of crowding of the organs in the space beneath the integument because of the sparsity of the parenchyma. Another distinctive character is the large size of the vitellaria and, especially, the coarseness of their follicles. The two characters are jointly responsible for the production of a pair of prominent lateral bulges in the second quarter of the body (Fig. 1 B).

The body of *S. compactum* is lanceolate, bluntly pointed anteriorly but

rounded posteriorly, 3·5 mm. long and 0·8 mm. in maximum breadth. The body is broadest in its second quarter, in the region of the vitellaria, and not posteriorly as in *S. elegans*, and, indeed, in most other species of the genus. The cuticle is thin and lacks spines, but species of *Styphlodora* may lose their spines as a result of fixation so that this observation does not preclude the possibility of their existence in the living trematode.

An ovoid oral sucker which surrounds the subterminal mouth is 0·3 mm. across, being thus relatively larger than in *S. elegans*. The ventral sucker, about 0·4 mm. in diameter, occupies a more posterior position than in *S. elegans*, its posterior rim extending well into the middle one-third of the body. Behind the mouth there is a short prepharynx and then the pharynx, about 0·22 mm. in diameter, and thus approaches in size that of the largest available specimens of *S. elegans*. The oesophagus is short and the bifurcation of the gut occurs well in front of the ventral sucker. The caeca are narrow but relatively long, reaching to the final one-sixth of the body, and they closely approximate to the lateral margins of the body because of the sparsity of the parenchyma (Fig. 1 B).

The gonads occupy similar positions relative to one another as in *S. elegans*, but the testes are slightly farther back in the body, most of the anterior testis being in the posterior half. The form of the testes is irregularly ovoid and the long axis of each one is longitudinal. The anterior testis has a lobed margin and measures 0·37 × 0·26 mm.; the posterior one has a smooth egg shape and measures 0·44 × 0·26 mm. The common genital pore is situated in the region between the ventral sucker and the bifurcation of the gut. An unarmed cirrus, which is longer than that of *S. elegans* and curved at the tip, protrudes from the cirrus sac, which is straight and extends dorsal to the ventral sucker. The vesicula seminis interna is not hour-glass shaped. The ovary is ovoid and measures 0·20 × 0·11 mm. It is situated between the cirrus sac and the posterior testis as in *S. elegans*. The metraterm is weakly muscular and glandular. The receptaculum seminis is large and is partially obscured by the folds of the uterus, which are both more numerous and more voluminous than in *S. elegans*. Eggs crowd the uterus, which occupies all the available space between the caeca and reaches almost to the integument posteriorly.

S. compactum more closely resembles species of the genus which inhabit the gut of the host (*S. serrata*, *S. lachesidis* and *S. nicolli*) than those which inhabit the liver, gall bladder, kidneys and ureters. It differs from species hitherto found in the stomach or intestine in the relatively posterior position of the testes, the existence of branches of the uterus in front of the anterior testis and the sizes of the oral and ventral suckers relative to one another and to the length of the body. In *S. serrata* and *S. nicolli* the oral suckers occupy 6·3 and 9·3–10·2 % of the length of the body, the ventral suckers 6·7–7·0 and 9·7–10·6 % respectively. In *S. lachesidis* the ventral sucker is 'about twice the size of the mouth sucker' (MacCallum, 1921). In *S. compactum* the oral and ventral suckers occupy respectively 8·6 and 11·4 % of the body length. This species, moreover, differs from all others of the genus in the shape of the body, the

nature of the vitellaria and (excepting, perhaps, *S. horridum*) in the sparsity of the parenchyma.

THE SPECIES OF THE GENUS *STYPHLODORA* LOOSS, 1899

The genus *Styphlodora* was proposed by Looss (1899) for the species *serrata* and *solitaria*. The latter species was referred by Odhner (1911) to the new genus *Styphlotrema* on account of the symmetrical arrangement of the testes, the extensive nature of the vitellaria, the form of the excretory ducts and the great thickness of the egg capsules. Odhner also suggested that *Distomum horridum* Leidy, 1850 and *D. similis* Sonsino, 1890 be placed in the genus *Styphlodora*. Other species which have been recorded since are *S. bascaniensis* Goldberger, 1911, *S. condita* De Faria, 1911, *S. najae* Nicoll, 1912, *S. persimilis* Nicoll, 1914, *S. lachesidis* MacCallum, 1921, *S. renalis* Tubangui, 1933, *S. nicolli* Bhalerao, 1936, *S. magna* Byrd & Denton, 1938, *S. natricis* Byrd & Denton, 1938 and *S. dentipharyngeata* Chatterji, 1940. Mehra (1931) proposed to remove *S. bascaniensis* from the genus and place it in a new genus, *Platymetra*, but Byrd & Denton (1938) have objected to this proposal on the grounds that the differences cited by Mehra are specific rather than generic.

There is some doubt, however, about the validity of the species *S. natricis*, which is based upon a single specimen. According to the authors, this form is more closely related to *S. magna* and *S. solitaria* than to other species. It is undoubtedly much more similar to the former than to the latter, and it was obtained from the same location in the same species of host (gall bladder of *Natrix sipedon sipedon* L.). Only a single specimen of each of these species, *Styphlodora magna* and *S. natricis* were obtained, plus a fragment of a second specimen of the former. The specimen of *S. natricis* has been badly mutilated. It is bent laterally, has at least one tear across the 'shoulders' and a somewhat telescoped posterior extremity. These defects can be held responsible for some of the characters on the basis of which specific distinction is claimed, namely, the position of the genital pore, the space between the fork of the gut and the ventral sucker, the position of the ovary and the tendency of the uterus to separate the ovary from the ventral sucker (see Fig. 3 D). The smaller size of *S. natricis* cannot be accounted of specific importance, as Byrd & Denton would like. It is 0·76 the length of *S. magna*, which is well within the size range of other species, e.g. *S. elegans*, in which the length of the smallest specimen amounts to only 0·34 that of the largest. Distortion of the body of *S. natricis* vitiates the measurements provided, so that slight differences of form may be more apparent than real. The relative sizes of the suckers vary in the two forms, but this may be taken as due to individual variation. Despite the fact that the ventral sucker of *S. elegans* is much larger than the oral one, the writer has encountered more than one instance in which the size relations are reversed because of artefacts. For these reasons as well as many similarities which need not be specified, the writer suggests that *S. natricis* be regarded as a synonym of *S. magna* (cp. C and D, Fig. 3).

Bhalerao (1936) has provided a key to the species of the genus *Styphlodora* which the writer has tried to use but without success. The characters selected by Bhalerao for the separation of species are the shapes and relative positions of the testes, the presence or absence of a prepharynx, the extent of the

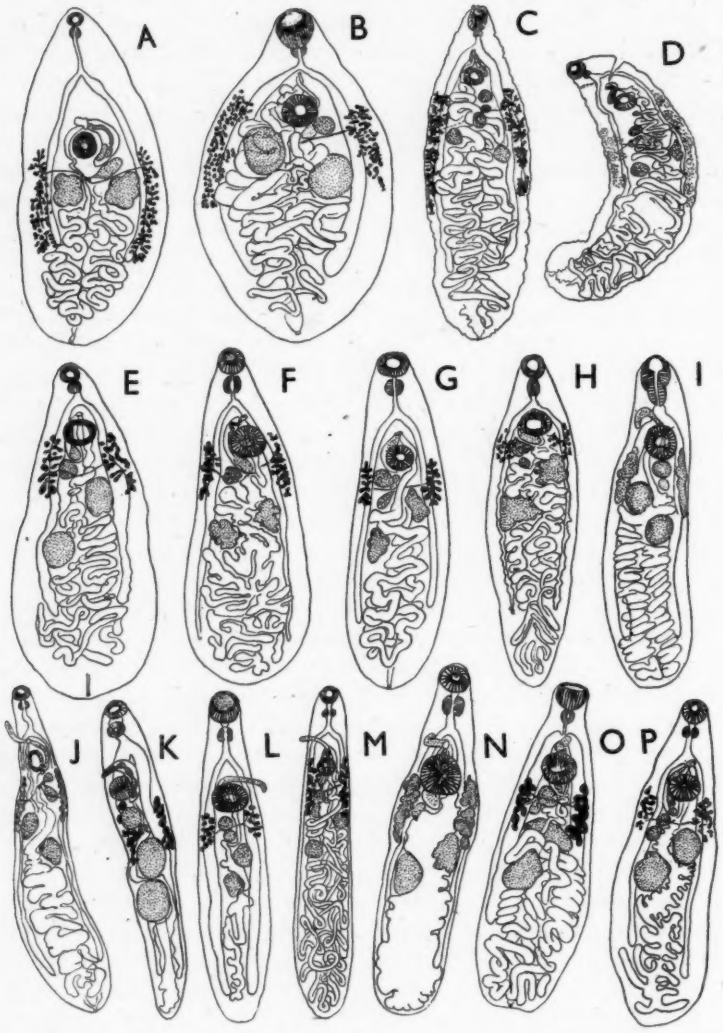

Fig. 3. The species of the genus *Styphlodora* Looss, 1899. A, *solitaria* (now in genus *Styphlotrema*); B, *bascaniensis*; C, *magna*; D, *natricis* (now relegated to synonymy with *magna*); E, *renalis*; F, *similis*; G, *serrata*; H, *persimilis*; I, *nicolli*; J, *lachesidis*; K, *dentipharyngeata*; L, *najae*; M, *horridum*; N, *compactum*; O, *condita*; P, *elegans*. The species are arranged in the order of their separation in the key.

vitellaria, the position of the ventral sucker and the length of the caeca. Some of these characters are of little value in this respect. Further, Bhalerao has misinterpreted the observations of various writers. Thus he states that the testes of *S. solitaria* (which lies outside the genus, as Odhner showed, but which is included in the key) are symmetrical, although Looss observed that the testes of his solitary specimen were 'fast auf gleicher Höhe, der linke um ein Geringes weiter nach vorn als der rechte'. *S. bascaniensis* and *S. similis* (Fig. 3 B, F) are said to have 'slightly oblique' testes, while other species are said to have testes which are 'distinctly oblique, their transverse zones separate'. It is significant that in sixty-three specimens of *S. elegans* there are nine instances of testes situated at distinct transverse zones, fifty-one instances of clearly overlapping testes, and three instances of almost exactly opposite testes. Further, Bhalerao claims that *S. persimilis* and *S. renalis* (Fig. 3 H, E) can be separated because of differences in the margins of the testes in the two species. In *S. persimilis* the testes are said to possess 'deep lobes', although Nicoll made no mention of this character and in his Fig. 5, Pl. II, shows testes that are only slightly lobed. In *S. renalis* the testes are said to be 'rounded or slightly lobed' which is in contradiction with Tubangui's statement that their surfaces 'are rarely smooth, often they are more or less distinctly indented so that each organ may present two to five lobes'. In nine specimens of *S. elegans* the testes are distinctly indented, although in more than fifty others their borders are smooth.

The lack of a prepharynx has been recorded for only two species of *Styphlodora*, *S. persimilis* and *S. renalis*. For the former, Nicoll states simply 'there is no prepharynx' and for the latter, Tubangui remarks 'prepharynx absent'. Nicoll observed, however, that the 'neck' of *S. persimilis* is short and adds that his specimens were somewhat contracted. In all species in which a prepharynx occurs this organ is very short and in some instances cannot be shown clearly in a figure, although there seems no reason why the pharynx should be shown overlapping the oral sucker by half its length in a form possessing a prepharynx, as is the case in Bhalerao's figure of *S. nicolli* (Fig. 3 I).

The position of the ventral sucker is no doubt a character of great value although, as the writer has shown, the relative size and position of this organ varies with total size of the body. The differences specified by Bhalerao for the separation of *S. nicolli* and *S. serrata* (Fig. 3 I, G) are the situations of the ventral sucker 'at one-fourth' and 'at one-third' of the length of the body respectively from the anterior end. Apart from the vagueness of this statement, the difference is within the range of variation shown by individuals of the same species, e.g. *S. elegans*. It is unlikely, however, that the trematode which Bhalerao obtained from the intestine of *Zamenis mucosus* in the Calcutta Zoo is identical with a species which was obtained from the gut of *Varanus niloticus* in the Leipzig Zoo, though Bhalerao has failed to separate the two species on morphological grounds in his key.

The vitellaria vary in extent in different species of *Styphlodora*, but

Bhalerao relies too much upon this character. Thus, *S. najae* (Fig. 3 L) is separated from five other species (Fig. 3 M, G, I, J) because the vitellaria end 'anterior to the testes'. In four of the five species (all except M) the vitellaria are said to extend 'only as far as the anterior testis', which amounts to a contradiction. One of the species is *S. condita*. Now, Nicoll stated that the vitellaria of *S. najae* extend 'from the posterior border of the ventral sucker to the anterior border of the left (i.e. anterior) testis' while, according to De Faria, the vitellaria of *S. condita* 'extend from the anterior border of the first testis to the posterior border of the ventral sucker'.

As species of *Styphlodora* cannot be separated by the use of Bhalerao's key, the writer has constructed an alternative key, in which a greater number and wider variety of characters are employed. In using the shapes of the body, sizes of the suckers, etc., as criteria by which separation of the species can be achieved, the writer has paid attention to the measurements and statements made by various authors rather than to their figures, and he has assumed that such measurements were made of specimens as little distorted as possible. Differences in the proportions of parts of the body of all the species of the genus which are arranged in the order of their separation in the key, are seen almost at a glance in Fig. 3 (B–P), where, by means of a camera lucida device, the diagrams of the various authors have been brought to approximately the same size, so that apparent absolute differences are also relative ones. Unfortunately no allowance can be made for changes in the proportions which result from growth because data are so scanty and incomplete.

A note on *Styphlodora horridum* (Leidy, 1850)

Certain assumptions have to be made in regard to this species, which was incorrectly described by Leidy, e.g. that the most posterior two of the four testes attributed to the species are truly the testes, that the anterior two are ovary and receptaculum seminis respectively, that the 'ovaries' are in reality the vitellaria, the 'pharynx' is prepharynx, the 'oesophageal bulb' pharynx, etc. That these assumptions are correct is shown, however, by scrutiny of the magnificent diagram (Fig. 1, Pl. 43). A much greater difficulty arises because Leidy states the range of lengths of his specimens ($1\frac{1}{2}$–$2\frac{3}{4}$ lines) but only single dimensions, which may refer to the specimen mentioned in the diagnosis. If this is so, the main dimensions of the trematode (translated into mm.) are: length 4·5, maximum breadth 1·27, diameters of oral and ventral suckers 0·24 and 0·25, length of prepharynx 0·08, length of spines 0·022, diameters of anterior and posterior testes 0·26 and 0·32, diameter of ovary 0·29 and dimensions of eggs $0{\cdot}035 \times 0{\cdot}019$. The breadth of the body may be erroneously stated, because it works out at 0·28 body length and because the figure shows it to be no more than 0·17 body length. In spite of such difficulties, we may assume safely that *S. horridum* is a species of slender form which has suckers and gonads of very small absolute and relative size.

Key to the species of the genus Styphlodora *Looss*, 1899

(1) Body oval or broadly lanceolate, maximum breadth generally more than one-third body length. Right and left testes separated by a wide median space.

(A) Oral sucker larger than ventral sucker. Genital pore at or near the level of the fork of the gut.

(*a*) Body very broad (breadth 44–59% length). Laurer's canal ends in a blind sac ... ... *bascaniensis*

(*b*) Body narrow (breadth less than 40% length). Laurer's canal opens to the exterior ... ... *magna*

(B) Oral sucker not larger than ventral sucker. Genital pore generally well behind the fork of the gut.

(*a*) Maximum breadth of body more than 35% length. Prepharynx absent. Oesophagus short, practically absent ... ... *renalis*

(*b*) Maximum breadth of body less than 35% length. Prepharynx present. Oesophagus clearly present ... ... *similis*

(2) Body narrowly lanceolate, maximum breadth generally less than one-third body length. Right and left testes generally not separated by a wide median space.

(A) Maximum breadth of body generally more than one-quarter length.

(*a*) Anterior end of body (to ventral sucker) relatively long. Bifurcation of gut well in front of ventral sucker. Eggs mostly larger than 0·042 × 0·021 mm. ... ... *serrata*

(*b*) Anterior end of body (to ventral sucker) relatively short. Bifurcation of gut immediately in front of ventral sucker. Eggs mostly smaller than 0·042 × 0·021 mm.

(*aa*) Suckers transversely oval. Ratio of diameters of oral and ventral suckers 5/6, always greater than 4/5, never greater than 6/7. Prepharynx absent ... ... *persimilis*

(*bb*) Suckers rounded. Ratio of diameters of oral and ventral suckers greater than 6/7. Prepharynx present ... ... *nicolli*

(B) Maximum breadth of body generally not more than one-quarter length.

(*a*) Anterior end of body acutely pointed, breadth at oral sucker less than 5% length of body. Oesophagus long (five times length of prepharynx). Ventral sucker twice as large as oral sucker and may be longitudinally oval ... ... *lachesidis*

(*b*) Anterior end of body bluntly pointed, breadth at oral sucker greater than 5% length of body. Oesophagus short. Ventral sucker less than twice as large as oral sucker.

(*aa*) Body thin and cylindrical or narrow and flattened dorso-ventrally. Suckers of approximately equal size. Genital pore well behind fork of gut.

(*aaa*) Ventral sucker provided with spines, pharynx with strong dentitions ... ... *dentipharyngeata*

(*bbb*) Ventral sucker without spines, pharynx without dentitions.

(*aaaa*) Caeca long, reaching almost to final one-tenth of body. Suckers large (about 10% body length). Uterus weakly developed ... ... *najae*

(*bbbb*) Caeca short and dilated posteriorly. Suckers small (much less than 10% body length). Uterus well developed ... ... *horridum*

(*bb*) Body with lateral swellings opposite vitellaria, sharply attenuated anteriorly. Oral sucker appreciably smaller than ventral sucker (ratio of diameters 3/4). Genital pore well behind fork of gut ... *compactum*

(*cc*) Body tapering anteriorly from its posterior half, posterior end rounded or truncated. Oral sucker smaller than ventral sucker. Genital pore near fork of gut.

(*aaa*) Both ends of body truncated. Ratio of diameters of oral and ventral suckers greater than 0·8. Oral sucker broader than 8% length of body. Testes of irregular shape, overlapping median line. Eggs shorter than 0·045 mm. ... ... *condita*

(*bbb*) Anterior end of body pointed, posterior end rounded. Ratio of diameters of oral and ventral suckers less than 0·8. Oral sucker narrower than 8% length of body. Testes ovoid, one on either side of median line. Eggs longer than 0·045 mm. ... *elegans*

Note. Host, location of trematode in body of host, and locality have been left out of account, although they also serve in the separation of the species.

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